Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia). 3. *Palaemon (Palaemon) longirostris* H. Milne Edwards, 1837 and the effect of antibiotic on morphogenesis

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Synopsis

The larval stages of *Palaemon* (*Palaemon*) *longirostris* are described from specimens reared in the laboratory with (+AB) and without (−AB) antibiotics. Growth in the early stages of larval development was enhanced by the use of antibiotics. There was also an increase in intermoult period and a two-moult delay of metamorphosis from 7 to 9 in +AB larvae. With these exceptions, the effect of antibiotics on morphogenesis was no more than expected in normal meristic variation. The relationship between moulting, growth and morphogenesis is examined in relation to genetic input, epigenesis and phenotypic variation in this estuarine species.

Introduction

The aim of this paper is twofold: to provide a complete description of the larval development of *Palaemon* (*Palaemon*) *longirostris* H. Milne Edwards, 1837 including the hitherto unknown zoea 4 and to assess both quantitative and qualitative effects of antibiotics on morphogenesis. Little attention has been given to the larval development of *P.* (*P.*) *longirostris* with the exception of papers by Gurney (1924*b*) and Korshelt (1944) in which zoeae 1–3, 5 and post larvae were described. The adults of this species are widely distributed in estuaries (Gurney, 1923; De Man, 1923) with records from the southern North Sea, west coast of Ireland and as far south as the Bay of Biscay (Fincham & Williamson, 1978). The species is also present in the Mediterranean and Black Seas. Larvae from plankton samples, however, are extremely rare (Gurney, 1924*b*; Williamson, personal communication). Personal observations on offshore, inshore and estuarine plankton samples which were collected from the North Sea and around the English and Welsh coasts by MAFF Fisheries Laboratory, Lowestoft, confirm these earlier findings.

Antibiotics are used routinely in the culture of larval decapods at the BM(NH) as an additive to the sea water to control build-up of bacteria in the compartmented rearing trays (Fincham, 1977, 1979). The effect of antibiotics on the development of brachyuran decapods has been investigated (Christiansen, 1971) but their effect on morphogenesis in natant decapods is less well known. Wickins (1972) compared the survival of *Palaemon serratus* (Pennant, 1777) larvae and the proportion which metamorphosed when cultured with and without antibiotics.

Materials and methods

Ovigerous *Palaemon* (*Palaemon*) *longirostris* were collected in July 1977 from filtering screens at the tidal water intake of the West Thurrock Electricity Generating Station on the River Thames (grid reference: TQ 593768). Rearing techniques similar to those reported previously (Fincham,1977, 1979) were used with the following modifications:

1. The controlled temperature room was at 18 ± 0·5 °C, equivalent to ambient water temperature at the time of collection.

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Table 1 Larval development and the effect of antibiotic on morphological variation in *Palaemon* (*Palaemon*) *longirostris*. (Figures in brackets refer to larvae reared with antibiotic.)
R = rudimentary; + = present/yes; − = absent/no

	Zoea/Moult							
	1	2	3	4	5	6	7	PL1(8)
Carapace								
No. of dorsal spines	0	1	2	3	3	3	3	6
	(0)	(1)	(2)	(3)	(3)	(3)	(3)	(3)
No. of ventral rostral spines	0	0	0	0	0	0	0–1	2
	(0)	(0)	(0)	(0)	(0)	(0)	(0–1)	(0–1)
Supraorbital spines +/−	−	+	+	+	+	+	+	−
	(−)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
No. of antero-lateral spines	0	1	2	2	2	2	2	2
	(0)	(1)	(2)	(2)	(2)	(2)	(2)	(2)
Rostrum tip – downturned +/−	−	+	+	+	+	+/−	+/−	−
	(−)	(+)	(+)	(+)	(+)	(+/−)	(+/−)	(+/−)
Ventral retrorse hooks +/−	+	+/−	+/−	−	−	−	−	−
	(+)	(+/−)	(+/−)	(−)	(−)	(−)	(−)	(−)
	one group				two groups			
Antenna 1								
No. of aesthetascs	1 Wide 2 narrow	2 Wide 2 narrow	3 Wide	3 Wide 1 narrow	3 Wide + 1 narrow; 2 narrow	4 Wide; 2 Wide	4 Wide; 2 Wide	3 Wide; 2 Wide
	(„)	(„)	(„)	(„)	(„)	(„)	(„)	(„)
Stylocerite +/−	−	R	+	+	+	+	+	+
	(−)	(R)	(+)	(+)	(+)	(+)	(+)	(+)
Statocyst +/−	−	−	−	R	+	+	+	+
	(−)	(−)	(−)	(R)	(+)	(+)	(+)	(+)
No. of segments, flagellum – Internal	0	(0)	1	1	1	2	3	6–9
	(0)	(0)	(1)	(1)	(1)	(2)	(3)	(3)
External	1	1	1	1	1	1	2	6
	(1)	(1)	(1)	(1)	(1)	(1–2)	(2)	(2)
Accessory flagellum +/−	−	−	−	−	−	−	−	R
	(−)	(−)	(−)	(−)	(−)	(−)	(−)	(−)
Antenna 2								
Endopodite – No. of segments	1	1	3	5	6–8	9–10	12–16	44+
	(1)	(1)	(3)	(5)	(6–8)	(9–15)	(13–15)	(13+)

Length of scaphocerite	1 : 1·4	1 : 1·2	1 : 0·9	⩽	<	<	<	<
	(1 : 1·4)	(1 : 1·2)	(1 : 0·9)	(⩽)	(<)	(<)	(<)	(<)
Exopodite – No. of distal segments	5	4–5	3	0	0	0	0	0
	(5)	(4–5)	(3)	(0)	(0)	(0)	(0)	(0)
No. of plumose setae	9+2	16+2–17+2	20+2–21+2	22+2–23+2	26–28	27–29	29–30	36–38
	(9+2)	(16+2)	(20+2)	(„)	(25+27)	(26–30)	(29–30)	(31–33)
External spine +/–	–	–	–	+	+	+	+	+
	(–)	(–)	(–)	(+)	(+)	(+)	(+)	(+)
Mandible – Lacinia mobilis +/–	+	+	+	+	+	+	+	–
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(–)
Palp	–	–	–	–	–	–	–	–
	(–)	(–)	(–)	(–)	(–)	(–)	(–)	(–)
Maxilla 1								
No. of endite setae – Coxa	6	6	6	7	7	8	8	8–9
	(6)	(6)	(6)	(7)	(7)	(8)	(8)	(8)
Basis	5	7	7	7–8	(8)	8	8	14–16
	(5)	(7)	(7)	(7–8)	(8)	(8)	(8–9)	(8–9)
Maxilla 2								
No. of endite setae – Coxa	4	4	4	4	4	4	4	0
	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)
Basis 1	3	3	3	3	3	3	4	6–7
	(3)	(3)	(3)	(3)	(3)	(3)	(4)	(4)
Basis 2	4	4	4	4	4	4	4	8
	(4)	(4)	(4)	(4)	(4)	(4)	(4–5)	(4–5)
Endopodite	3	3	3	3	3	3	3	1
	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)
No. of plumose setae – Exopodite	5	7	9–11	12–13	(19–20)	22–25	25–28	30–33
	(5)	(7)	(10–11)	(15–17)	(17–22)	(24–26)	(25–28)	(27–28)
Maxilliped 1								
No. of setae on internal margin – Coxa	1	1	1	1	1	1	1	6–7
	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)
Basis	6	6	6	6	6	7	7–8	27–30
	(6)	(6)	(6)	(6)	(6)	(7)	(7–8)	(7–8)
Exopodite – No. of proximo-lateral setae	0	0	0	0	0	3	5–6	8–9
	(0)	(0)	(0)	(0)	(0)	(4)	(5–6)	(6)
Maxilliped 2								
Endopodite – No. of segments	4	4	4	4	4	4	4	5
	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)

Table 1 (*cont.*)

	Zoea/Moult							
	1	2	3	4	5	6	7	PL1(8)
Exopodite +/−	+	+	+	+	+	+	+	+
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Setae +/−	+	+	+	+	+	+	+	+
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Maxilliped 3								
Endopodite – No. of segments	4	5	5	5	5	5	5	4
	(4)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
Exopodite +/−	+	+	+	+	+	+	+	R
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Setae +/−	+	+	+	+	+	+	+	+
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Pereiopods 1 & 2 +/−	R	+	+	+	+	+	+	+
	(R)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Biramous +/−	+	+	+	+	+	+	+	R
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Endopodite – Propodus fixed finger +/−	−	−	+	+	+	+	+	+
	(−)	(−)	(+)	(+)	(+)	(+)	(+)	(+)
Pereiopod 3 +/−	R	R	R	+	+	+	+	+
	(R)	(R)	(R)	(+)	(+)	(+)	(+)	(+)
Biramous +/−	+	+	+	+	+	+	+	R
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Pereiopod 4 +/−	R	R	R	+	+	+	+	+
	(R)	(R)	(R)	(+)	(+)	(+)	(+)	(+)
Biramous +/−	−	−	−	−(R)	−	−	−	−
	(−)	(−)	(−)	(−)	(−)	(−)	(−)	(−)

Pereiopod 5 +/−	R	R	+	+	+	+	+	+
	(R)	(R)	(+)	(+)	(+)	(+)	(+)	(+)
Biramous +/−	−	−	−	−	−	−	−	−
	(−)	(−)	(−)	(−)	(−)	(−)	(−)	(−)
Abdomen								
Somite 5 – lateral spines +/−	−	+	+	+	+	+	+	R
	(−)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Somite 6 – 'Continuous' with telson +/−	+	+	−	−	−	−	−	−
	(+)	(+)	(−)	(−)	(−)	(−)	(−)	(−)
Pleopods +/−	−	−	R	R	R	R	R	+
	(−)	(−)	(R)	(R)	(R)	(R)	(R)	(R)
Fringing setae			−	−	−	−	R	+
			(−)	(−)	(−)	(−)	(R)	(R)
Appendix interna 2–5 +/−			−	−	−	R	+	+
			(−)	(−)	(−)	(R)	(+)	(+)
Telson								
Posterior margin concave (−) or	+/−	+/−	(−)	−	−	+/−	+/−	+
convex (+)	(+/−)	+/−	(−)	(−)	(−)	(+/−)	(+/−)	(+/−)
Spine formula	7+7	7+7	[1]6+6[1]	[1]6+6[1]	[3]4+4[3]	4+4	4+4	2+2
	(7+7)	(7+7)	([1]6+6[1])	(,,)	(,,)	(,,)	(,,)	(4+4)
Small spines +/−	+	+	+	+	+	+/−	−	−
	(+)	(+)	(+)	(+)	+	(+/−)	(−)	(−)
No. of pairs of lateral spines	0	0	0	0	0	3	3	3
	(0)	(0)	(0)	(0)	(0)	(3)	(3)	(3)
Uropods +/−	−	−	+	+	+	+	+	+
	(−)	(−)	(+)	(+)	(+)	(+)	(+)	(+)
Long plumose setae – Endopodite			0	12–13	17–19	20–21	23–26	28–31
			(0)	(12–13)	(17–20)	(20–25)	(20–25)	(24–26)
Exopodite			12–13	18+1–20+1	20+1–23+1	24+1–26+1	26+1–28+1	29–30
			(12+13)	(19+1–20+1)	(21+1–25+1)	(25+1–28+1)	(25+1–28+1)	(26+1–28+1)

2. Salinity of the water in the circulating system and the water used in the compartmented trays was adjusted to the conditions prevailing in the estuary (salinity varied from 10 to 17‰ at West Thurrock – laboratory salinity maintained at 14‰).
3. In 6 rearing trays, each with 18 compartments, a mixture of 50 i.u. benzylpenicillin (sodium) and 0·05 mg streptomycin sulphate per ml sea water was used instead of streptomycin sulphate alone.
4. A replicate series of trays was set up with no antibiotic in the sea water. The length of intermoult period, growth rate and meristic characters could then be compared with larvae reared with antibiotics.

Larval material has been deposited in the Crustacea collection of the BM(NH), registration number 1978: 307.

Palaemon (Palaemon) longirostris H. Milne Edwards, 1837

Palaemon longirostris H. Milne Edwards, 1837.
Palaemon edwardsii Heller, 1863.
Leander edwardsii Czerniavsky, 1884.
Leander longirostris De Man, 1915.
Leander longirostris Gurney, 1924*b*.
Palaemon (*Palaemon*) *longirostris* Holthuis, 1950.

SYNOPSIS OF LARVAL DATA FROM PUBLISHED WORK. *Leander longirostris* Gurney, 1924*b*: Figs 1–7 (zoeae 1–3, 5, post larvae 1, 2) laboratory reared and plankton; *Leander longirostris* Korschelt, 1944: Figs 810, 811 (zoeae 1–3) (after Gurney).

In the following short descriptions of the key characters of the larval stages, all setal counts have been omitted but these are recorded in Table 1.

DESCRIPTION OF LARVAL STAGES

Key characters are printed in *italic type* and are useful for separating stages of British species.

ZOEA 1 (Fig. 1) 3·5 mm (3·3–3·8 mm)*.

Head (Figs 1a, b): *eyes sessile.*

Carapace (Figs 1a, b): *without spines*, rostrum straight, tapering distally, ventral margin with minute retrorse teeth distally; *rostrum as long as or longer than antenna 1* (excluding terminal aesthetascs and setae).

Antenna 1 (Fig. 1c): peduncle bearing single flagellar segment, with three aesthetascs distally, one wide and two narrow.

Antenna 2 (Fig. 1d): exopod as a broad lamina divided into 5 (occasionally 6) segments distally; *endopodite of 1 segment.*

Mandibles (Fig. 1e): asymmetrical.

Maxillipeds 1–3 (Figs 1h–j): with natatory exopods.

Pereiopods 1, 2 (Figs 1k, l): *rudimentary, biramous.*

Pereiopod 3 (Fig. 1m): *minute biramous bud.*

Pereiopods 4, 5 (Figs 1n, o): minute uniramous buds.

Abdomen (Figs 1a, b): *somite 5 with posterior margin rounded*, not produced into spines; somite 6 continuous with telson. No trace of pleopods.

Telson (Figs 1p, q): fans out distally, posterior margin bears 7+7 plumose spines, inner pairs with longitudinal rows of scale-like spinules, decreasing in size on the plumose setae towards the edge of the fan; minute spines between four innermost pairs of plumose setae.

ZOEA 2 (Fig. 2) 3·9 mm (3·8–4·1 mm)

Head (Figs 2a, b): *eyes stalked.*

Carapace (Figs 2a, b): *one dorso-medial and a pair of supraorbital spines* all bent forward with small retrorse teeth, *rostrum without teeth, downturned at end to form a small hook.*

* Lengths of larvae reared without antibiotic quoted throughout; for comparison of larval growth rates with and without antibiotic see Fig. 18.

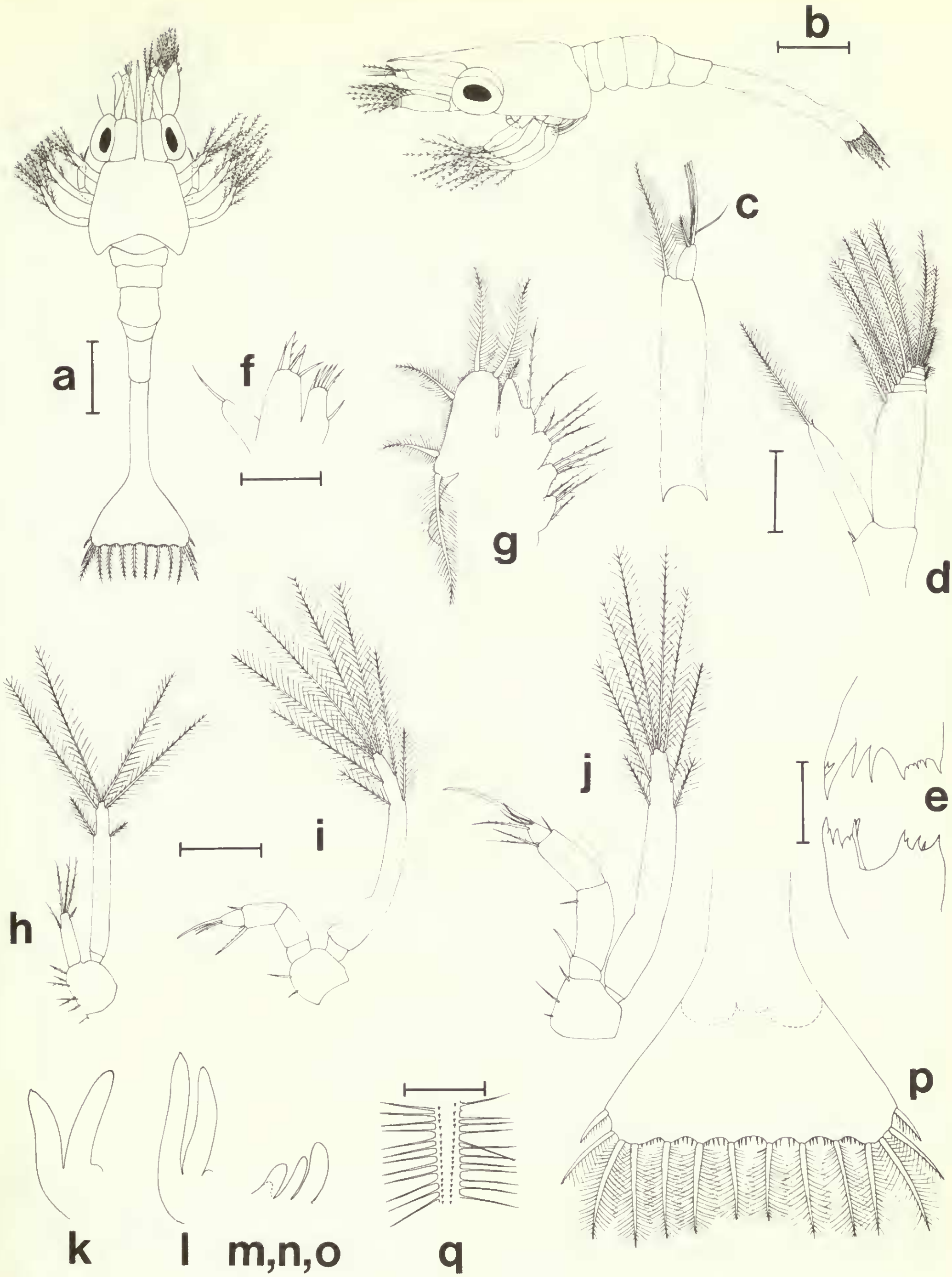

Fig. 1 Zoea 1: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson; (q) detail from inner pair of telsonic spines. Bar scales: a, b = 0·5 mm; c, d, h–p = 0·2 mm; f, g = 0·1 mm; e, q = 0·05 mm.

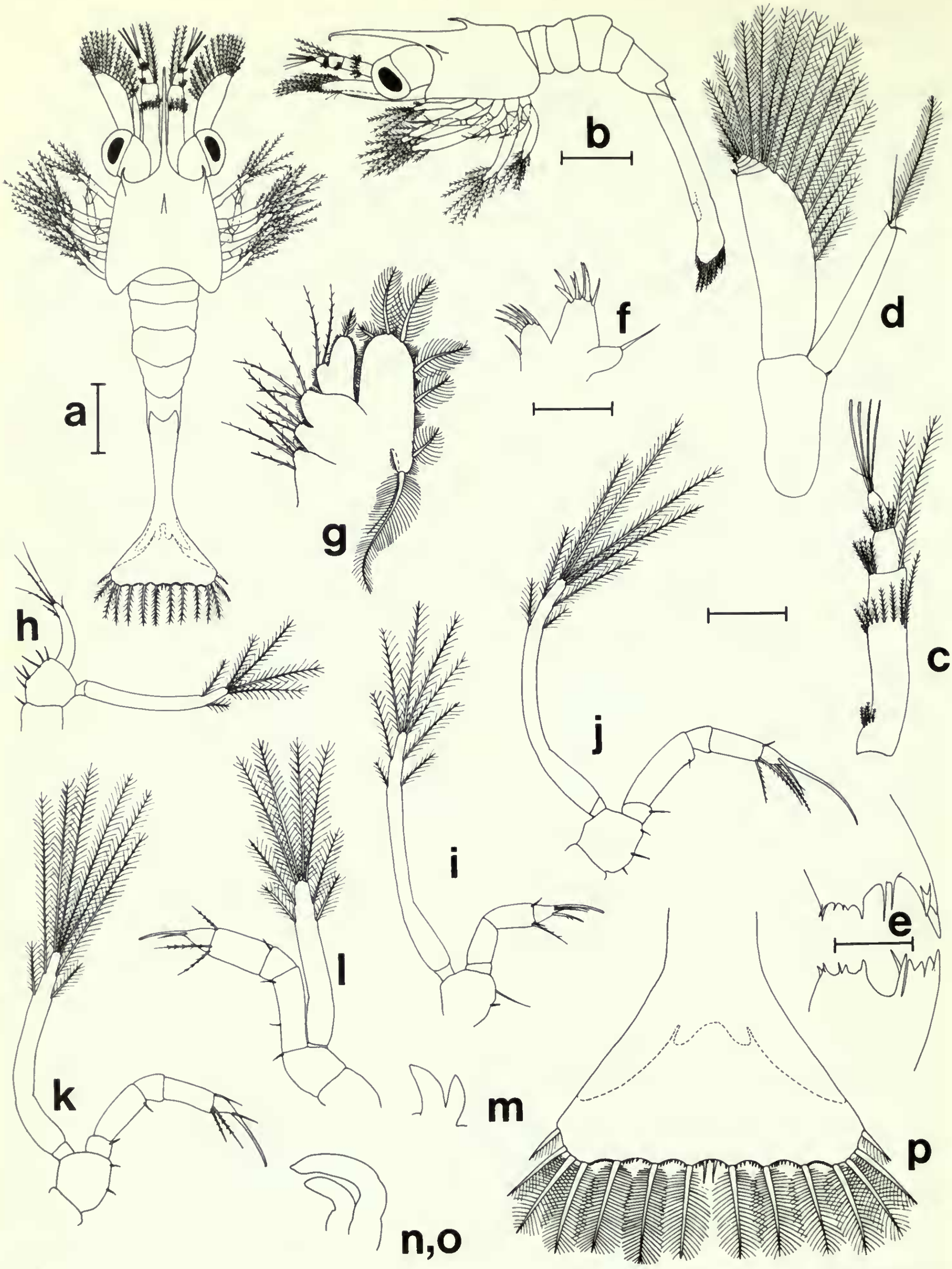

Fig. 2 Zoea 2: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0·5 mm; c, d, h–p = 0·2 mm; f, g = 0·1 mm; e = 0·05 mm.

Antenna 1 (Fig. 2c): *two peduncle segments, stylocerite forming on proximal external margin of first segment; single flagellar segment with four terminal aesthetascs, two wide and two narrow.*

Antenna 2 (Fig. 2d): exopodite with distal part divided into 4 or 5 segments; wide gap between 9 distal setae and new setae added at this moult.

Pereiopods 1, 2 (Figs 2k, l): *developed, with natatory exopodite.*

Pereiopod 3 (Fig. 2m): *rudimentary, biramous.*

Pereiopods 4, 5 (Figs 2n, o): *rudimentary, uniramous.*

Abdomen (Figs 2a, b): *somite 5 with posterior margin produced into a pair of conspicuous spines, somite 6 continuous with telson.*

Telson (Fig. 2p): *developing uropods visible beneath exoskeleton* alongside telson proper; *in central group of small spines, one pair longer than others.*

ZOEA 3 (Figs 3, 4) 4·5 mm (4·2–4·7 mm)

Carapace (Fig. 3a, b): *two dorso-medial spines* and pair of small fronto-lateral spines at edge of carapace beneath eyes, former with retrorse teeth; rostrum still downturned at end to form a small hook.

Antenna 1 (Fig. 4a): *conspicuous spine medially*, stylocerite more pronounced; distal segment of peduncle bearing *first segment of internal flagellum*, single segment of *external flagellum bearing 3 wide aesthetascs distally.*

Antenna 2 (Fig. 4b): expodite with distal part divided into 3 short segments; *endopodite of 3 segments.*

Pereiopods 1, 2 (Figs 4f, g): *endopodite with internal distal margin of propodus produced slightly forward* (will become fixed finger of chela).

Pereiopod 4 (Fig. 4i): *rudimentary, uniramous.*

Pereiopod 5 (Fig. 4j): *developed, uniramous.*

Abdomen (Figs 3a, b, 4k): somites 1–5 with rudimentary pleopods, *somite 6 divided from telson by suture. Uropod endopodite with no marginal setae, exopodite with marginal setae.*

Telson (Fig. 4k): narrower but still broader distally, outer pair of spines on posterior margin considerably reduced.

ZOEA 4 (Figs 5, 6) 5·2 mm (4·7–5·5 mm)

Carapace (Figs 5a–d): *three dorso-medial spines* with retrorse teeth; *rostrum still downturned at end to form a small hook.*

Antenna 1 (Fig. 5h): rudiment of circular statocyst visible on first segment of peduncle; *single segment of external flagellum bearing 3 wide and 1 narrow aesthetascs distally.*

Antenna 2 (Fig. 5i): endopodite of 5 segments and as long or longer than the exopodite; distal part of exopodite no longer divided into short segments *but with a stout terminal tooth on outer distal edge.*

Pereiopods 1, 2 (Figs 6d, e): *endopodite with internal distal margin of propodus produced forward to about half length of dactylus* (excluding terminal setae).

Pereiopod 3 (Fig. 6f): *developed, with natatory exopodite.*

Pereiopod 4 (Fig. 6g): *developed, exopod absent or bud-like.*

Abdomen (Figs 5a, b, 6i): *uropod exopodite and endopodite both with marginal plumose setae.*

Telson (Fig. 6i): a little broader distally than proximally; spine formula as in Zoea 3 but further reduction in size of two outer pairs of spines.

ZOEA 5 (Figs 7, 8) 5·8 mm (4·8–6·1 mm)

Carapace (Figs 7a, b): *rostrum still downturned to form small hook.*

Antenna 1 (Fig. 7c): single external flagellum with 4 aesthetascs distally, *with additional group of 2 aesthetascs on internal margin.*

Antenna 2 (Fig. 7d): *endopodite of 6–8 segments*, longer than exopodite.

Pereiopods 1, 2 (Figs 8d, e): *endopodite with internal distal margin of propodus produced forward to over half length of dactylus* (excluding terminal setae).

Pereiopod 4 (Fig. 8g): *exopod absent.*

Abdomen (Fig. 7b): *pleopods on somites 1–5 rudimentary, biramous.*

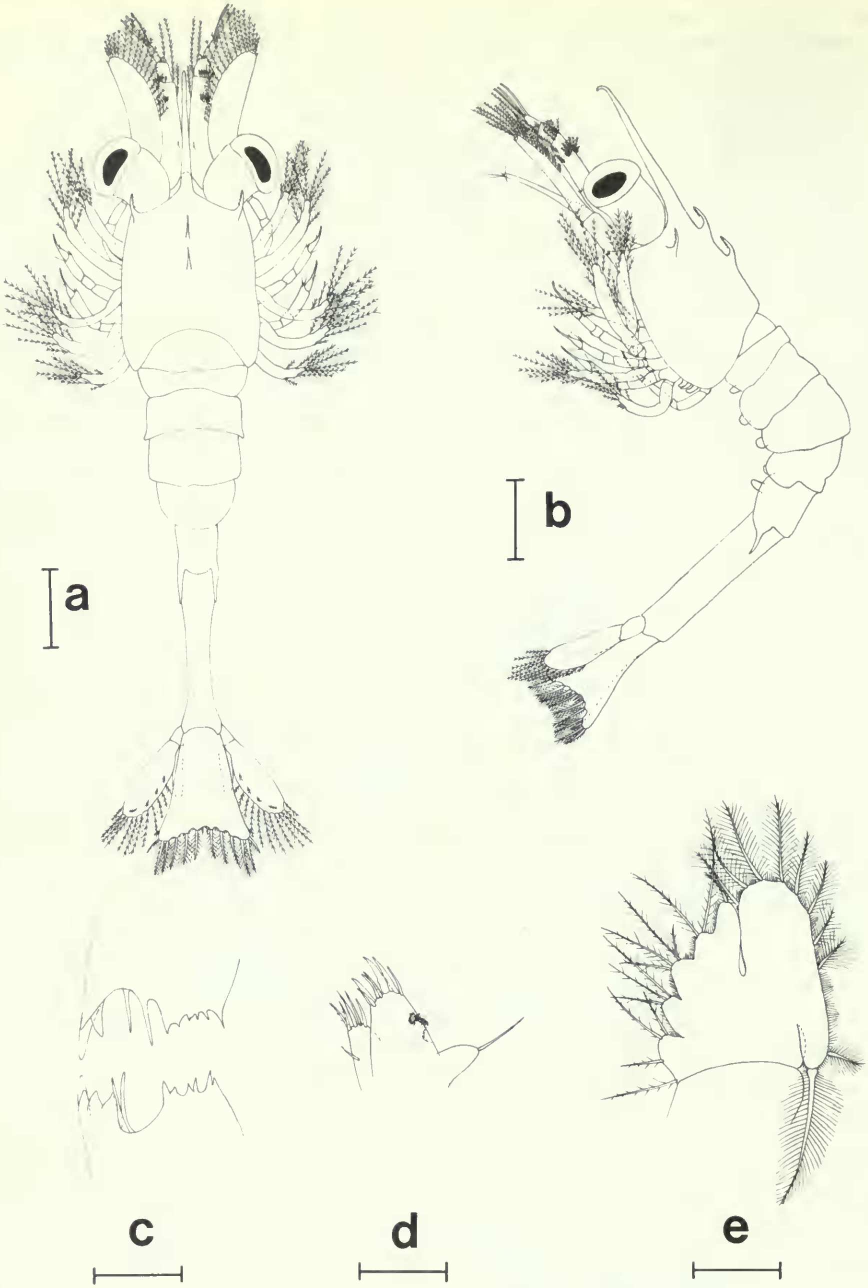

Fig. 3 Zoea 3: (a) dorsal view; (b) lateral view; (c) mandibles; (d) maxilla 1; (e) maxilla 2. Bar scales: a, b = 0·5 mm; c = 0·05 mm; d, e = 0·1 mm.

Telson (Fig. 8n): almost parallel sided; *spine formula* [*3*] *4+4* [*3*], some of small outer spines occasionally missing, posterior margin weakly concave, length about one-third overall length of telson.

Zoea 6 (Figs 9, 10) 6·3 mm (6·1–6·6 mm)

Carapace (Fig. 9a): *short plumose seta in angle of anterior dorso-medial spine, rostrum still downturned to form small hook.*

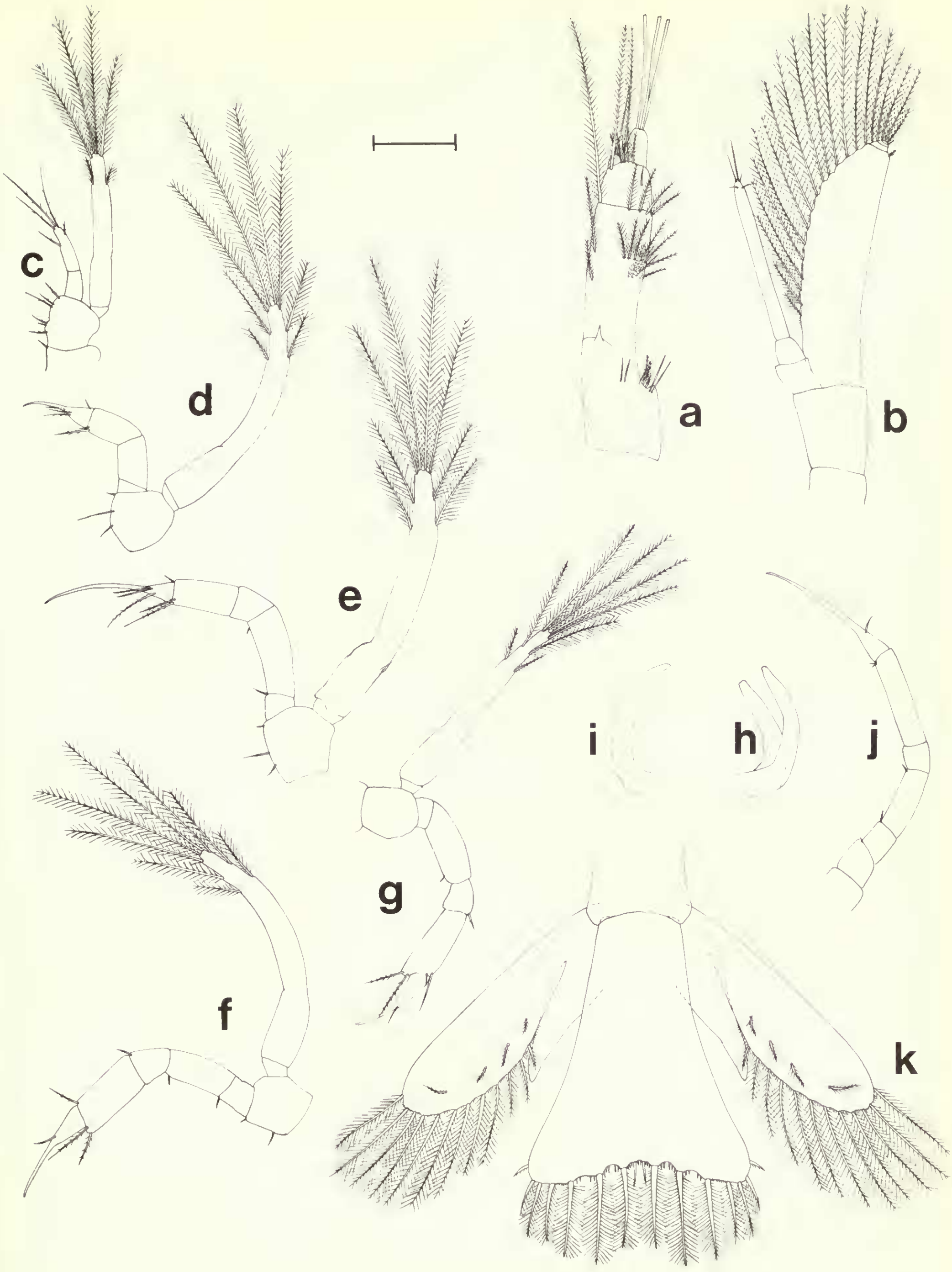

Fig. 4 Zoea 3: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) telson. Bar scale = 0·2 mm.

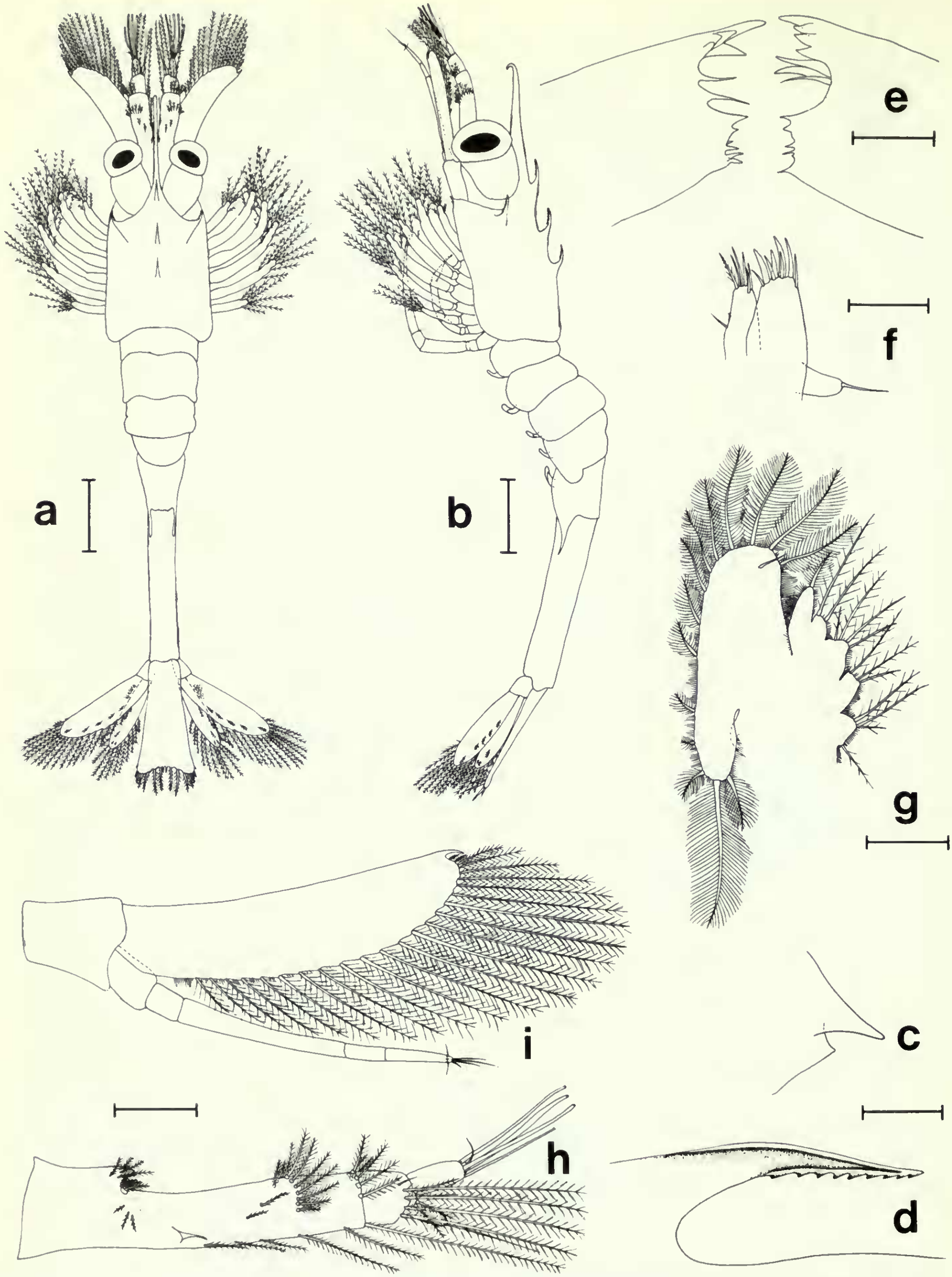

Fig. 5 Zoea 4: (a) dorsal view; (b) lateral view; (c) antero-lateral teeth of carapace; (d) first dorso-medial carapace spine; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) antenna 1; (i) antenna 2. Bar scales: a, b = 0·5 mm; c–e = 0·05 mm; f, g = 0·1 mm; h, i = 0·2 mm.

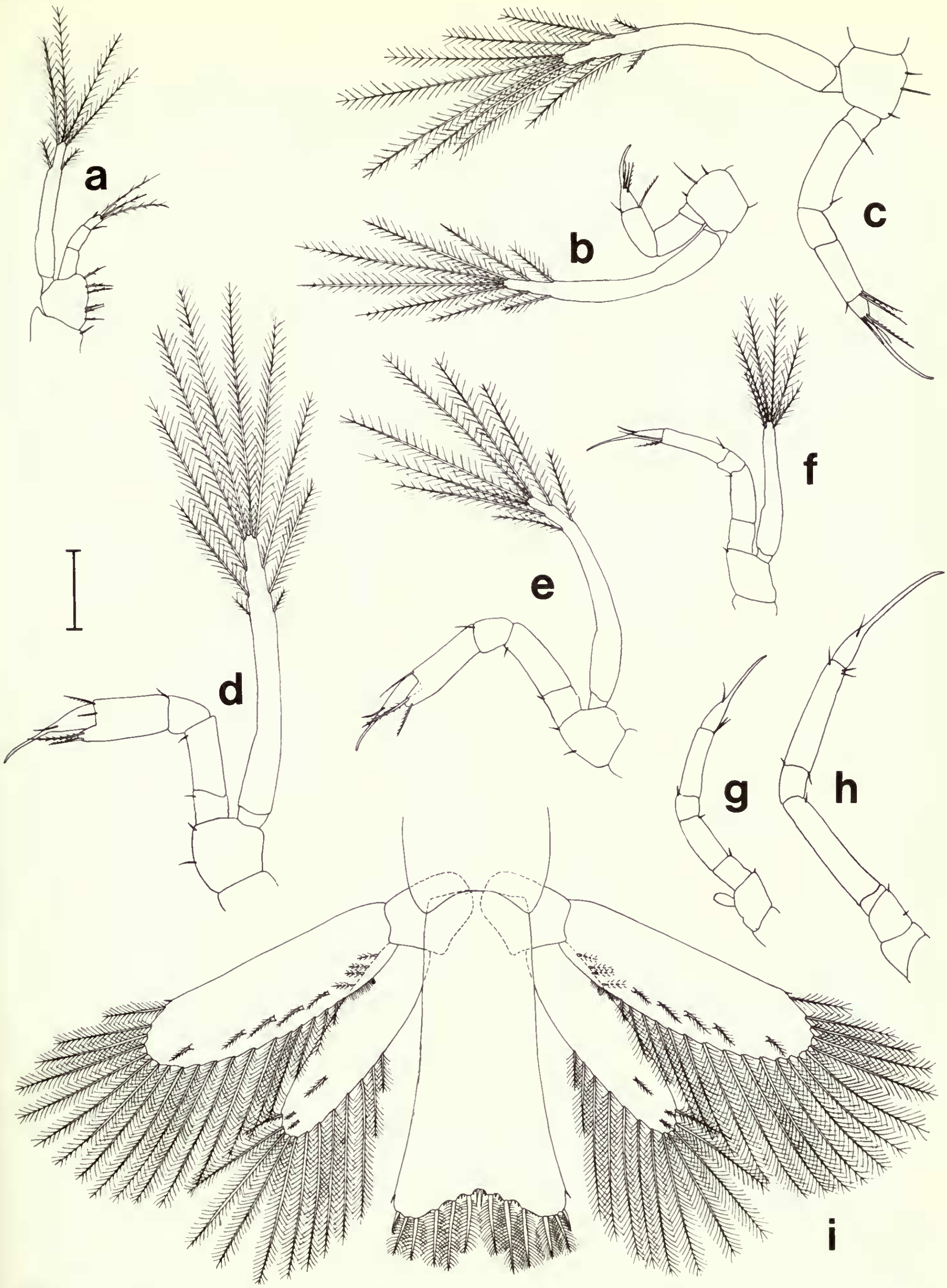

Fig. 6 Zoea 4: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e) pereiopod 2; (f) pereiopod 3; (g) pereiopod 4; (h) pereiopod 5; (i) telson. Bar scale = 0·2 mm.

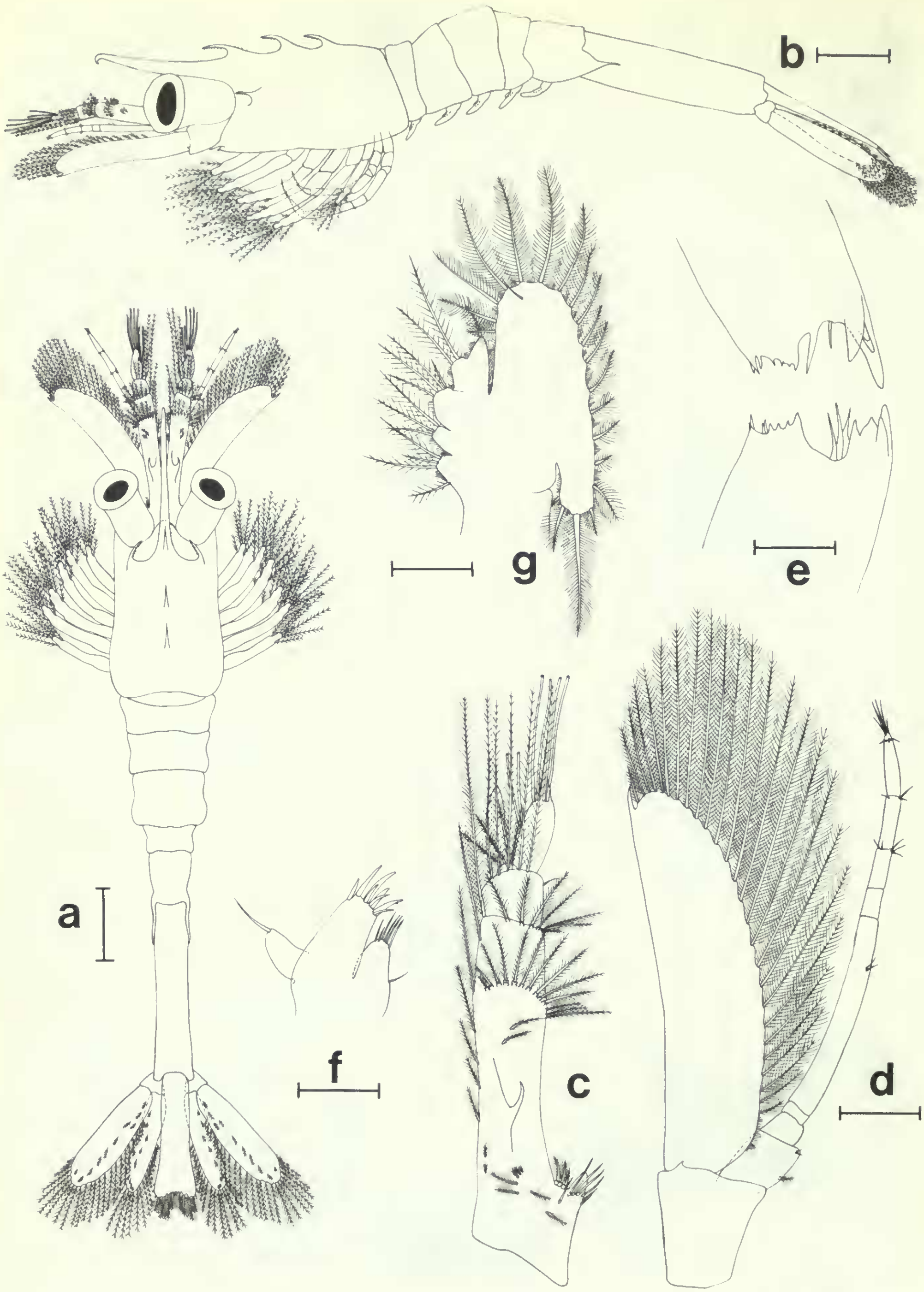

Fig. 7 Zoea 5: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2. Bar scales: a, b = 0·5 mm; c, d = 0·2 mm; e = 0·05 mm; f, g = 0·1 mm.

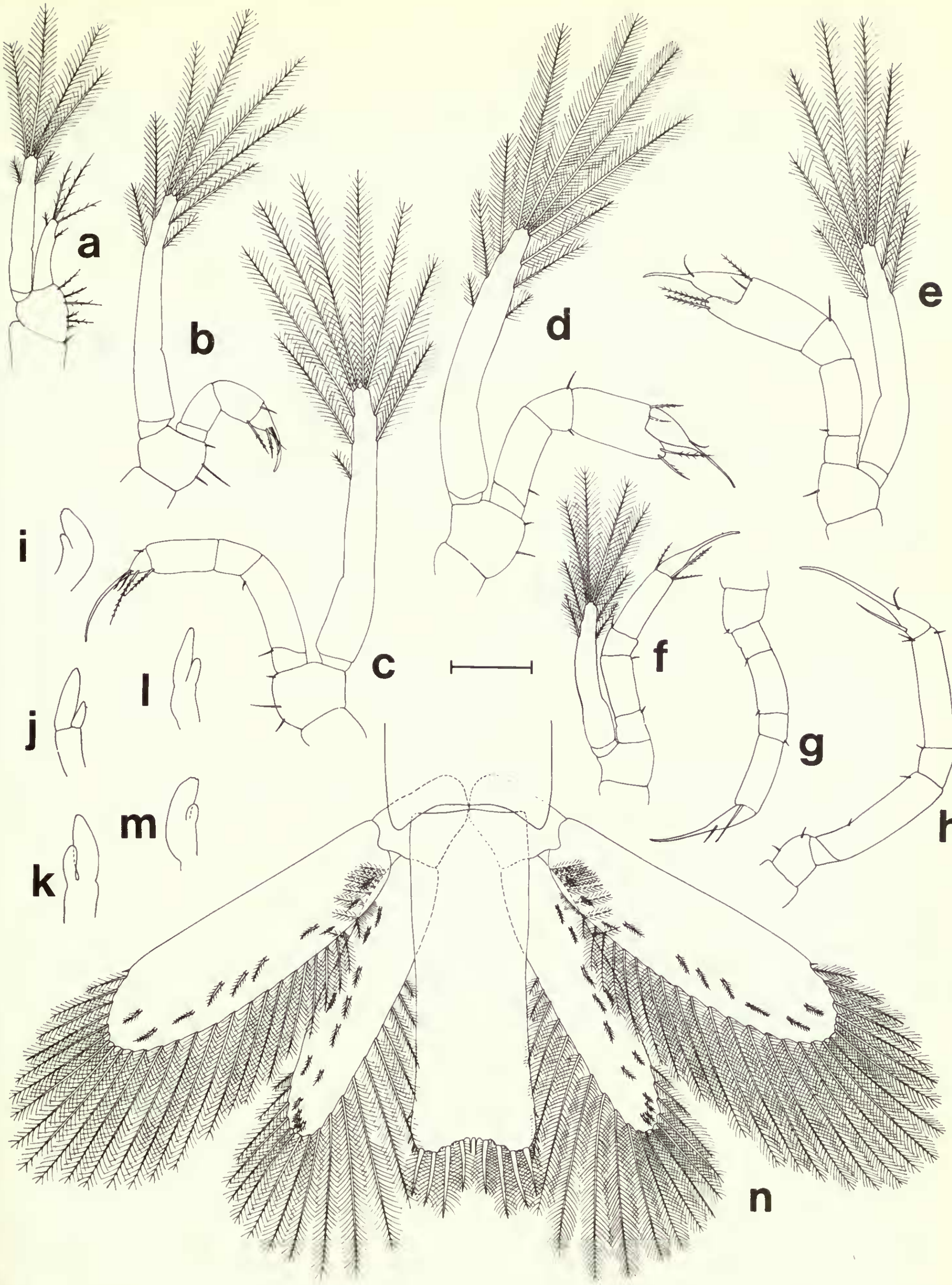

Fig. 8 Zoea 5: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e) pereiopod 2; (f) pereiopod 3; (g) pereiopod 4; (h) pereiopod 5; (i) pleopod 1; (j) pleopod 2; (k) pleopod 3; (l) pleopod 4; (m) pleopod 5; (n) telson. Bar scale = 0·2 mm.

Antenna 1 (Fig. 9c): internal flagellum of two segments.

Antenna 2 (Fig. 9d): *endopodite of at least 9 segments.*

Maxilliped 1 (Fig. 10a): *exopodite with 3* (usually) *proximo-lateral plumose setae.*

Pereiopods 1, 2 (Figs 10d, e): *endopodite with immovable finger of propodus produced forward to almost length of dactylus* (excluding terminal setae).

Abdomen (Figs 9b, 10i–m): *pleopods with rudimentary setae on margins of endopodite and exopodite*, endopodite of pleopods 2–5 with rudimentary appendix interna.

Telson (Fig. 10n): *narrowing distally*, posterior margin weakly convex and *length just over a quarter overall length of telson; small spines between large spines reduced in number to a central pair.*

Zoea 7 (Figs 11–13) 6·5 mm (6·3–6·8 mm)

A few specimens have already metamorphosed to post larvae at this moult. Meristic characters from these post larvae have not been included in Table 1 nor in the following description.

Carapace (Fig. 11a): rostrum with weak distal hook or straight, occasionally a single ventral tooth.

Antenna 1 (Fig. 12a): *internal flagellum of 3 segments, external flagellum of 2 segments.*

Antenna 2 (Fig. 12b): *endopodite of at least 12 segments.*

Maxilliped 1 (Fig. 12f): exopodite with 5 (usually) proximo-lateral plumose setae.

Pereiopods 1, 2 (Figs 13a, b): *propodus 'palm' almost as wide as long* (0·8 : 1).

Telson (Fig. 13k): *no small spines between large spines.*

Post larva 1 (Figs 14–17) 6·7 mm (6·3–7·1)

More than 50% of specimens have metamorphosed to post larvae at this moult. Meristic characters from the post larvae only have been included in Table 1.

Carapace (Figs 14a, b, 15b): *rostrum usually with 6 dorsal and 2 ventral teeth*, rostral tip straight (see intermediate condition of rostrum Fig. 15a) *supraorbital spines missing.*

Antenna 1 (Fig. 15c): internal flagellum of 6–9 segments and external flagellum of 6 segments, *distal group of aesthetascs reduced to three.*

Antenna 2 (Fig. 15d): endopodite multisegmented, several times longer than the scaphocerite.

Mandible (Figs 16a, b): *divided into pars incisiva and pars molaris*, lacinia mobilis no longer present and palp (three-jointed in adult) not yet appeared.

Maxilla (Fig. 16c): up to 16 setae on basal endite.

Maxilla 2 (Fig. 16d): *complete loss of setae on coxal endite and a reduction to 1 seta on endopodite*, increases in setae on basal endites.

Maxilliped 1 (Fig. 15e): large increase in setae on internal margin of basis (zoea 7: 7–8, post larva 1: 27–30).

Maxilliped 2 (Fig. 15f): endopodite with dactylus, propodus and merus flattened, *exopodite shortened and with reduced plumose setae.*

Maxilliped 3 (Fig. 15g): endopodite dactylus shortened, *exopodite reduced* to less than half the length of endopodite.

Pereiopods 1, 2 (Figs 16e, f): ischium, merus and carpus lengthened, *exopodite reduced* to less than length of ischium of endopodite, plumose setae much reduced.

Pereiopod 3 (Fig. 16g): endopodite dactylus tapering evenly distally, other joints lengthened, *exopodite reduced*, extending less than halfway along ischium of endopodite, plumose setae much reduced.

Pereiopods 4, 5 (Figs 16h, i): endopodite dactylus tapering evenly distally, other joints lengthened.

Pleopod 1 (Fig. 17a): *ratio of endopodite to exopodite 1 : 3·5*, endopodite bearing terminal plumose setae, exopodite fringed with long plumose setae.

Pleopods 2–5 (Figs 17b–e): endopodite over half length of exopodite, both with long, marginal plumose setae, endopodite with appendix interna bearing well-developed intero-distal coupling hooks.

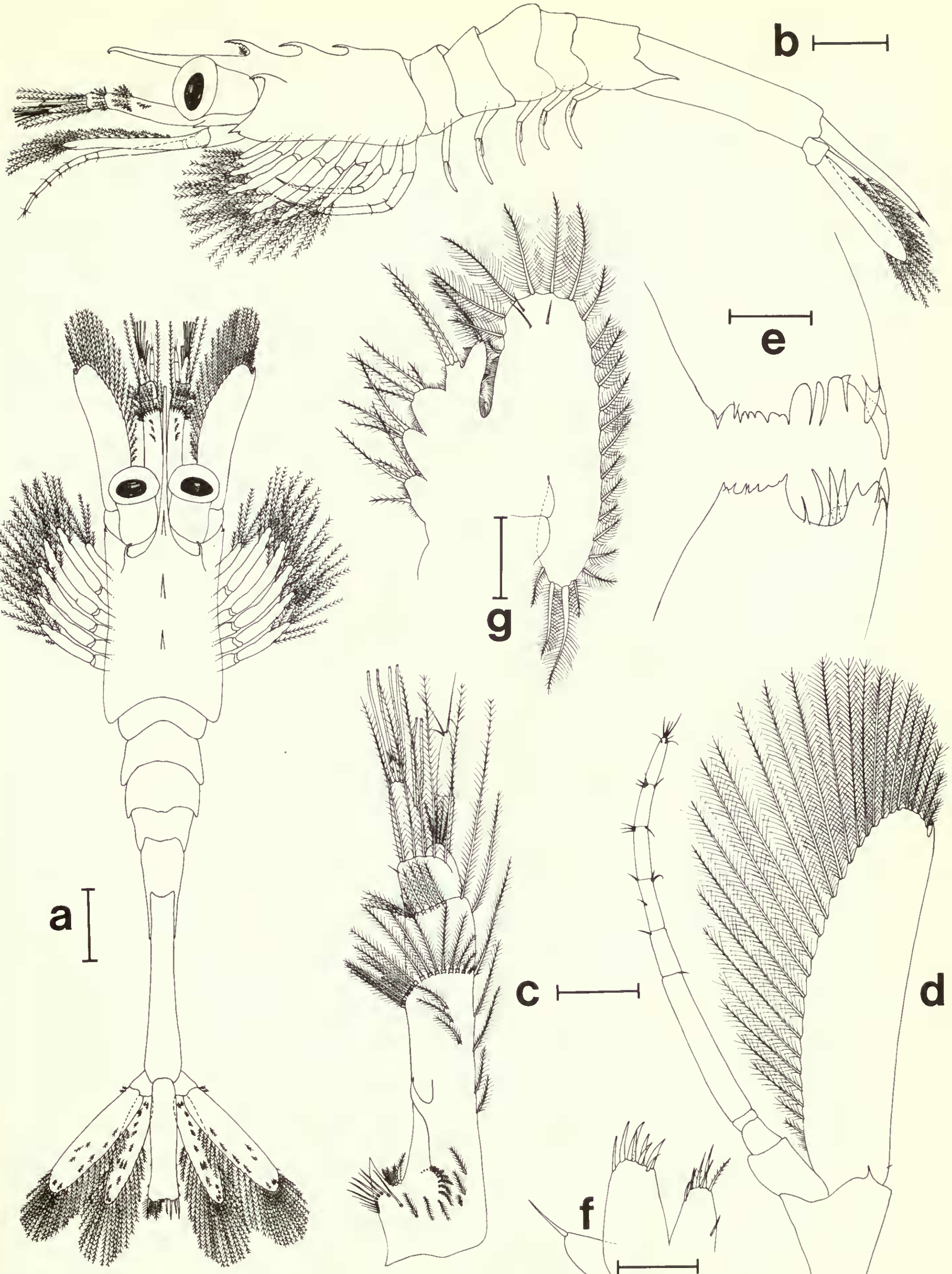

Fig. 9 Zoea 6: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2. Bar scales: a, b = 0·5 mm; c, d = 0·2 mm; e = 0·05 mm; f, g = 0·1 mm.

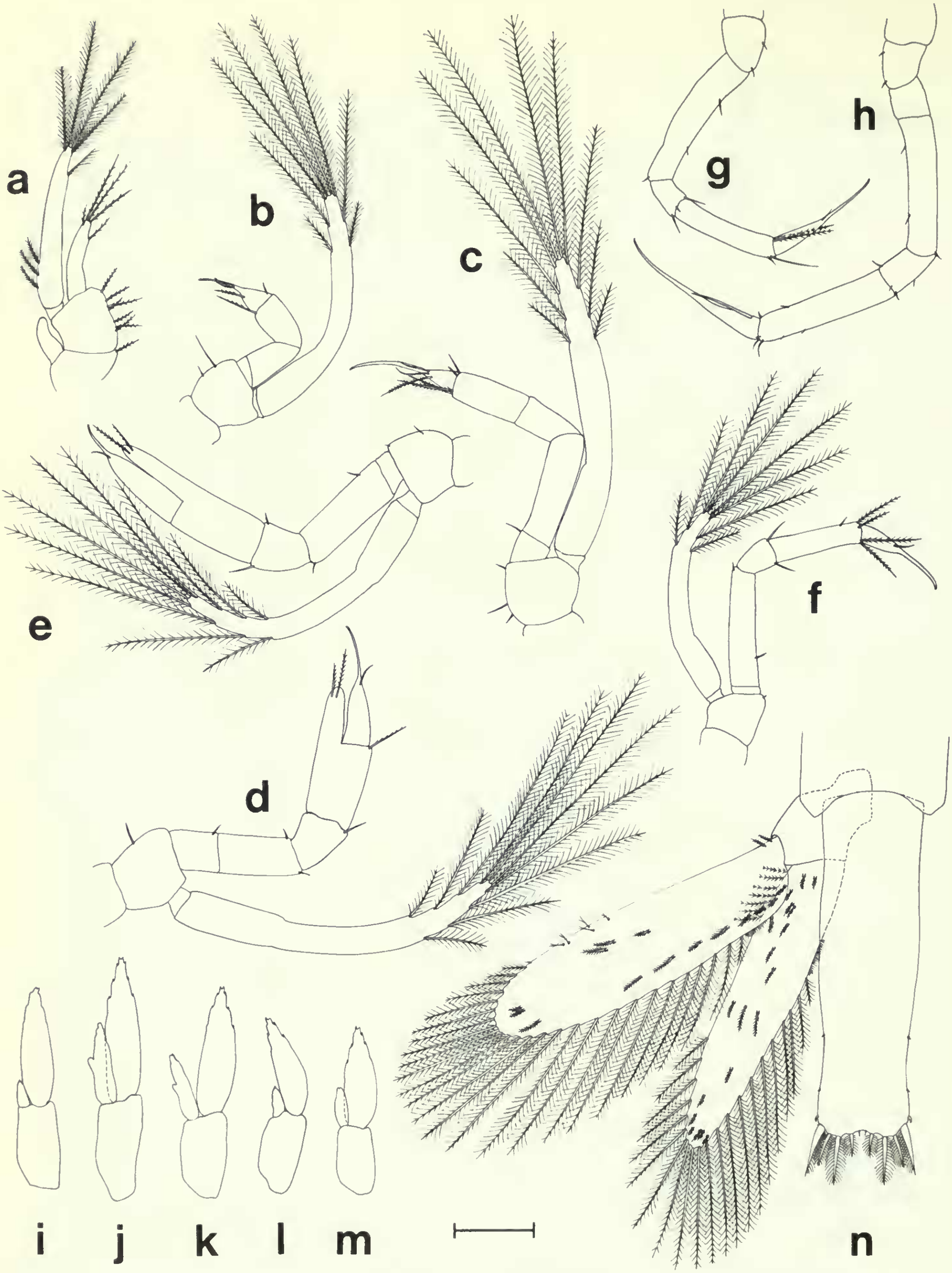

Fig. 10 Zoea 6: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e)pereiopod 2; (f) pereiopod 3; (g) pereiopod 4; (h) pereiopod 5; (i) pleopod 1; (j) pleopod 2; (k) pleopod 3; (1) pleopod 4; (m) pleopod 5; (n) telson. Bar scale = 0·2 mm.

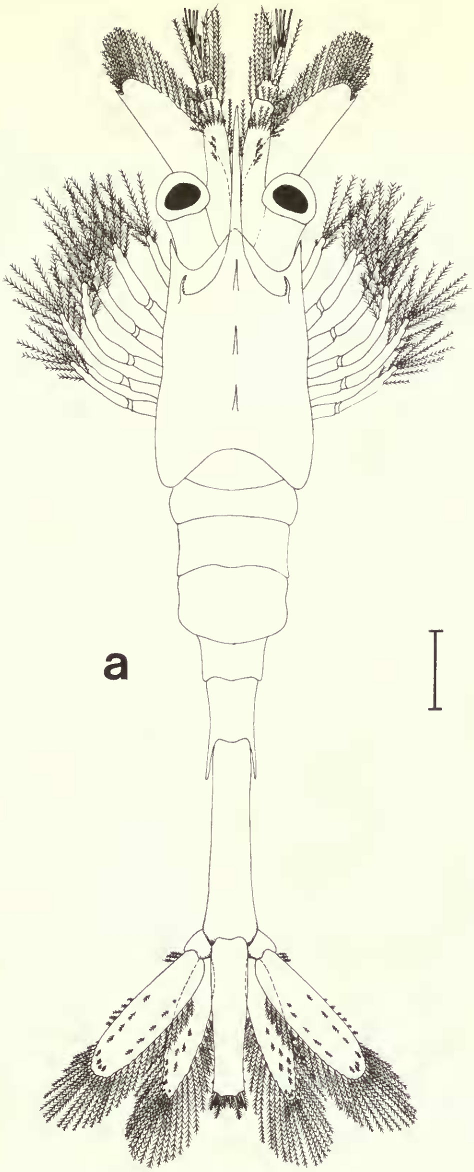

Fig. 11 Zoea 7: (a) dorsal view; (b) lateral view. Bar scale = 0·5 mm.

Abdomen (Fig. 14b): *fifth abdominal somite truncated,* point of stages 2–7 much reduced.

Telson (Fig. 17f): *extremely narrow, posterior margin tapering to a point* and bearing a pair of small (outer) and large (inner) spines and medially a pair of plumose setae. Two pairs of stout spines developed on lateral margins of telson (see intermediate condition found in specimens with intermediate rostral form Fig. 17g).

Effect of antibiotic

The effect of antibiotic on the length of intermoult period on two series each of 108 larvae kept at 18 °C is shown in Fig. 17a. Larvae reared without antibiotic (−AB) moult in less than 5 days to stage 3 compared with larvae reared with antibiotic (+AB) which take an average of

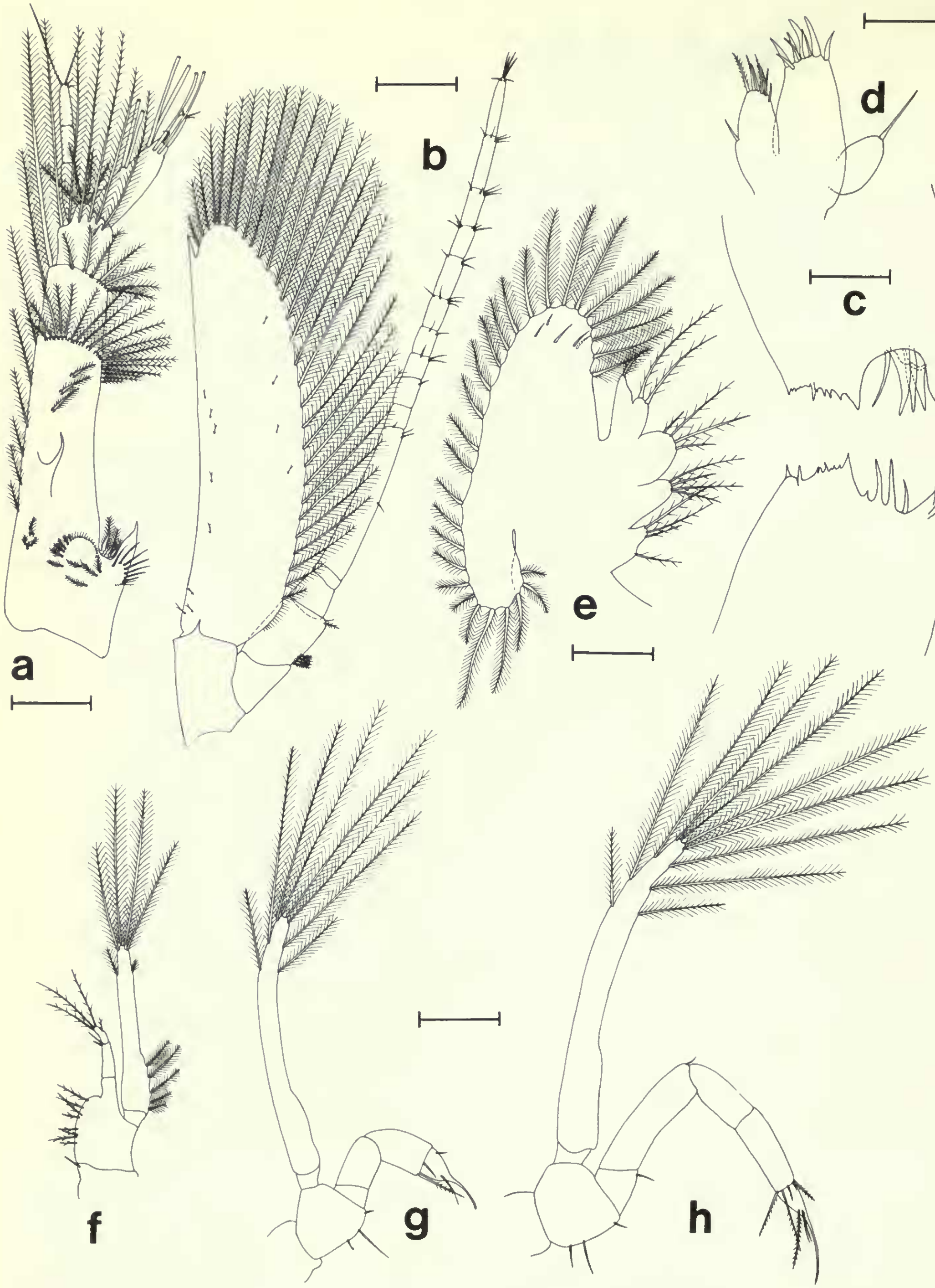

Fig. 12 Zoea 7: (a) antenna 1; (b) antenna 2; (c) mandibles; (d) maxilla 1; (e) maxilla 2; (f) maxilliped 1; (g) maxilliped 2; (h) maxilliped 3. Bar scales: a, b, f–h = 0·2 mm; c = 0·05 mm; d, e = 0·1 mm.

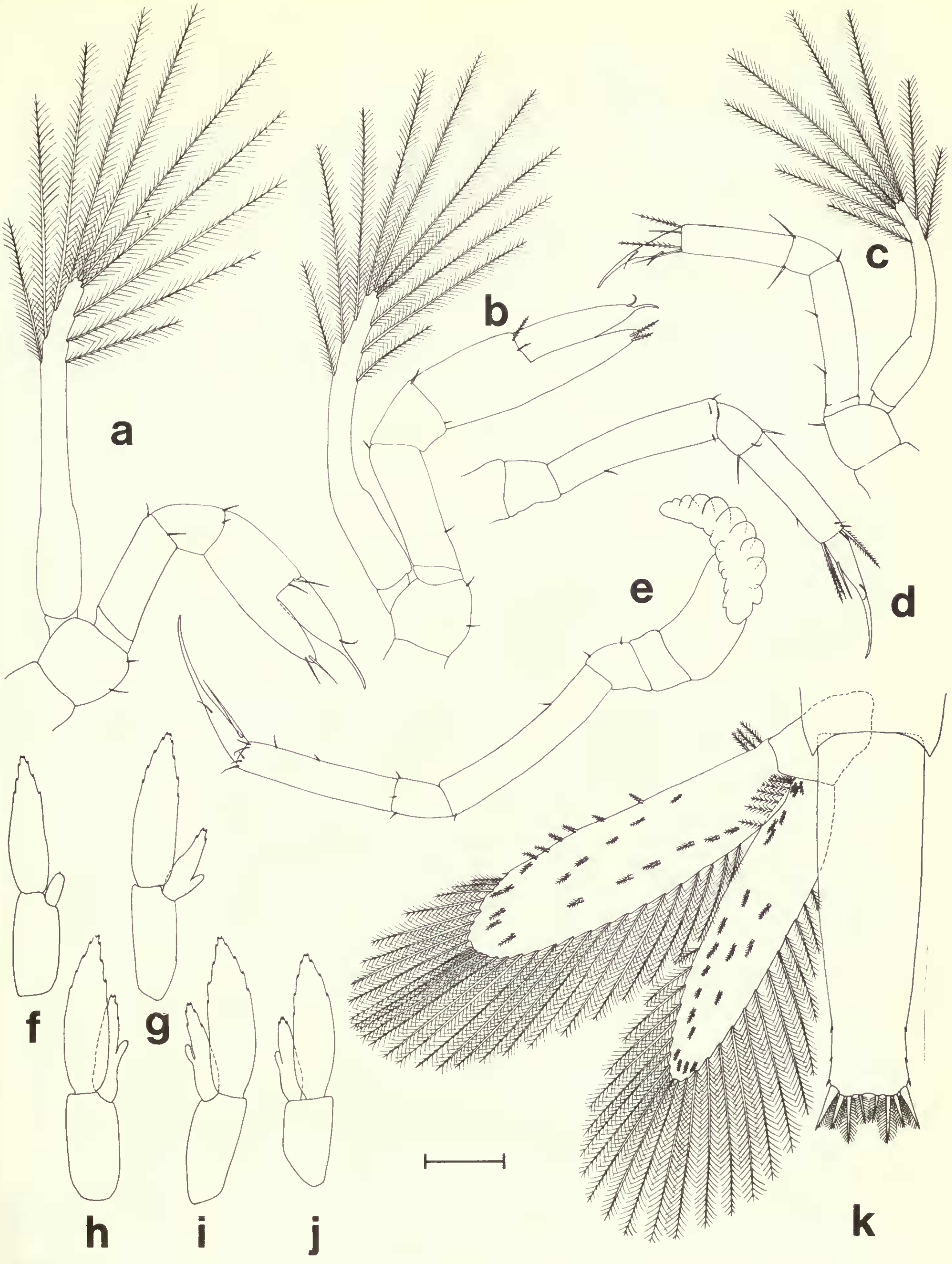

Fig. 13 Zoea 7: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) pereiopod 5; (f) pleopod 1; (g) pleopod 2; (h) pleopod 3; (i) pleopod 4; (j) pleopod 5; (k) telson. Bar scale = 0·2 mm.

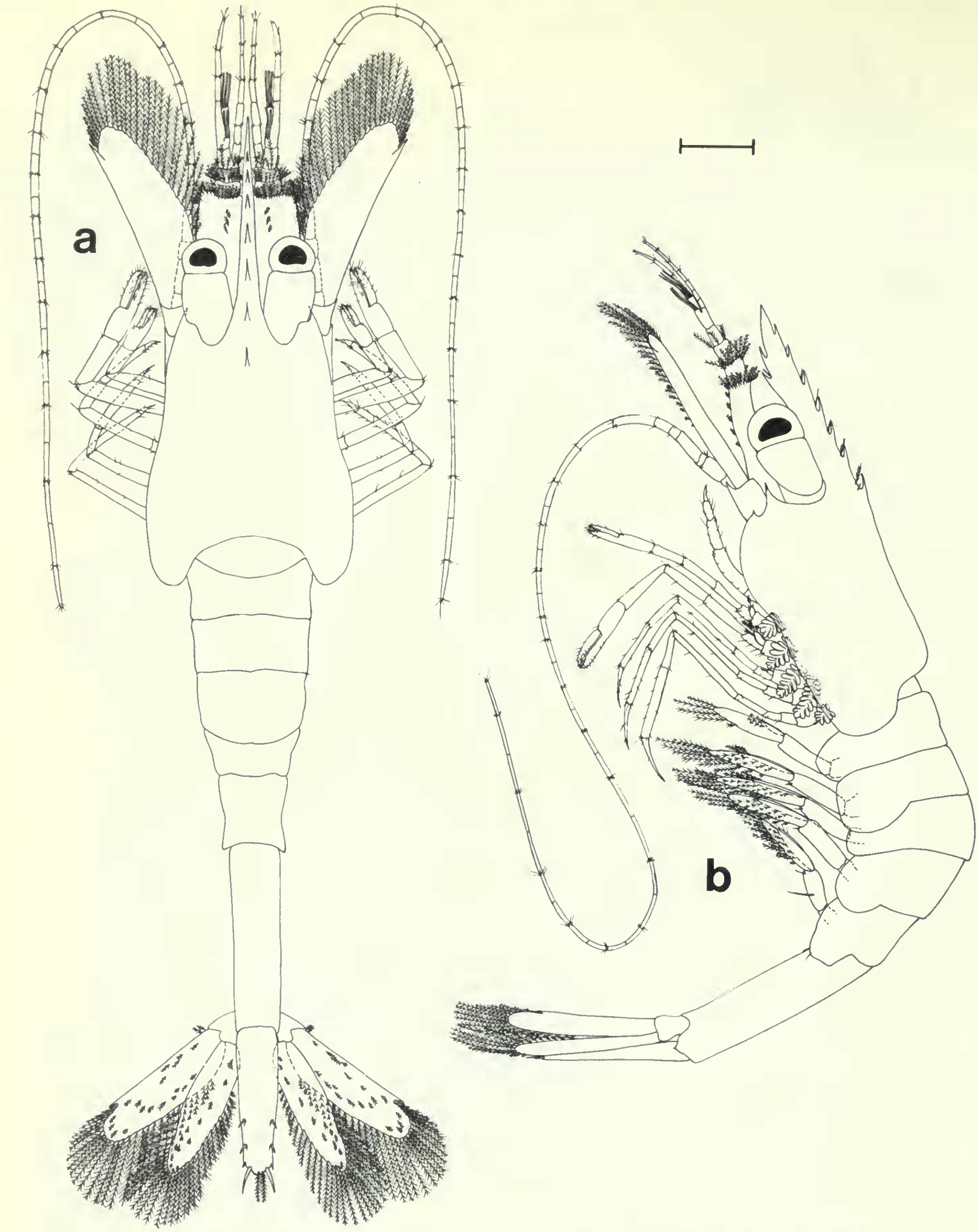

Fig. 14 Post larva 1: (a) dorsal view; (b) lateral view. Bar scale = 0·5 mm.

nearly 7 days. This advantage is maintained throughout the remaining period of larval development. Post larval stage is reached by at least 50% of −AB larvae at moult 7–8; metamorphosis is delayed until moult 9–10 in +AB larvae.

Fig. 17b shows the growth of the two series of larvae. Faster growth is shown by +AB larvae until stage 4 when −AB larvae overtake them in size. This increase is maintained throughout larval development with the two series coming close at moult 8. From this moult the difference in growth widens markedly, −AB larvae further increasing their average size over +AB larvae.

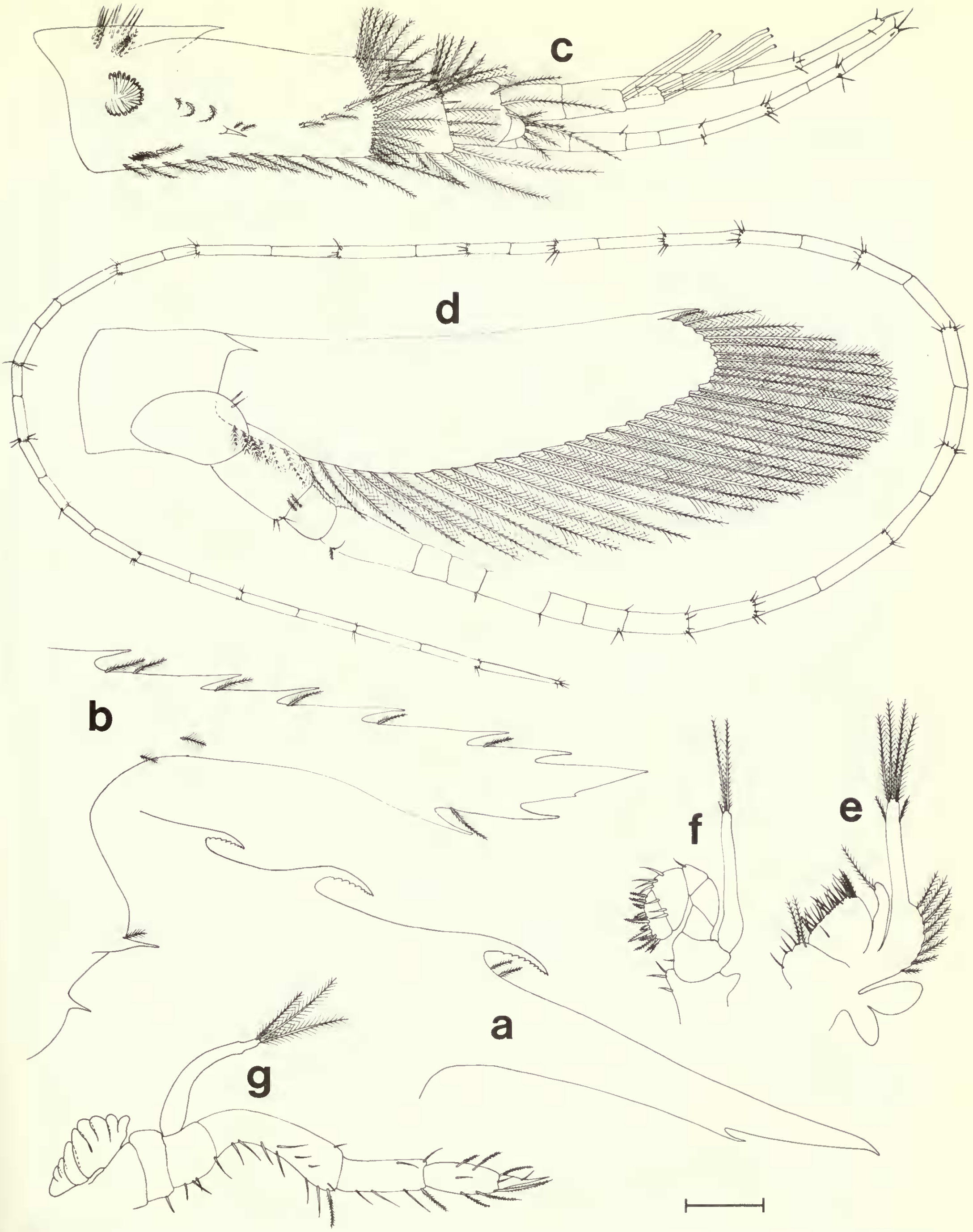

Fig. 15 Intermediate stage: (a) rostrum. Post larva 1: (b) rostrum; (c) antenna 1; (d) antenna 2; (e) maxilliped 1; (f) maxilliped 2; (g) maxilliped 3. Bar scale = 0·2 mm.

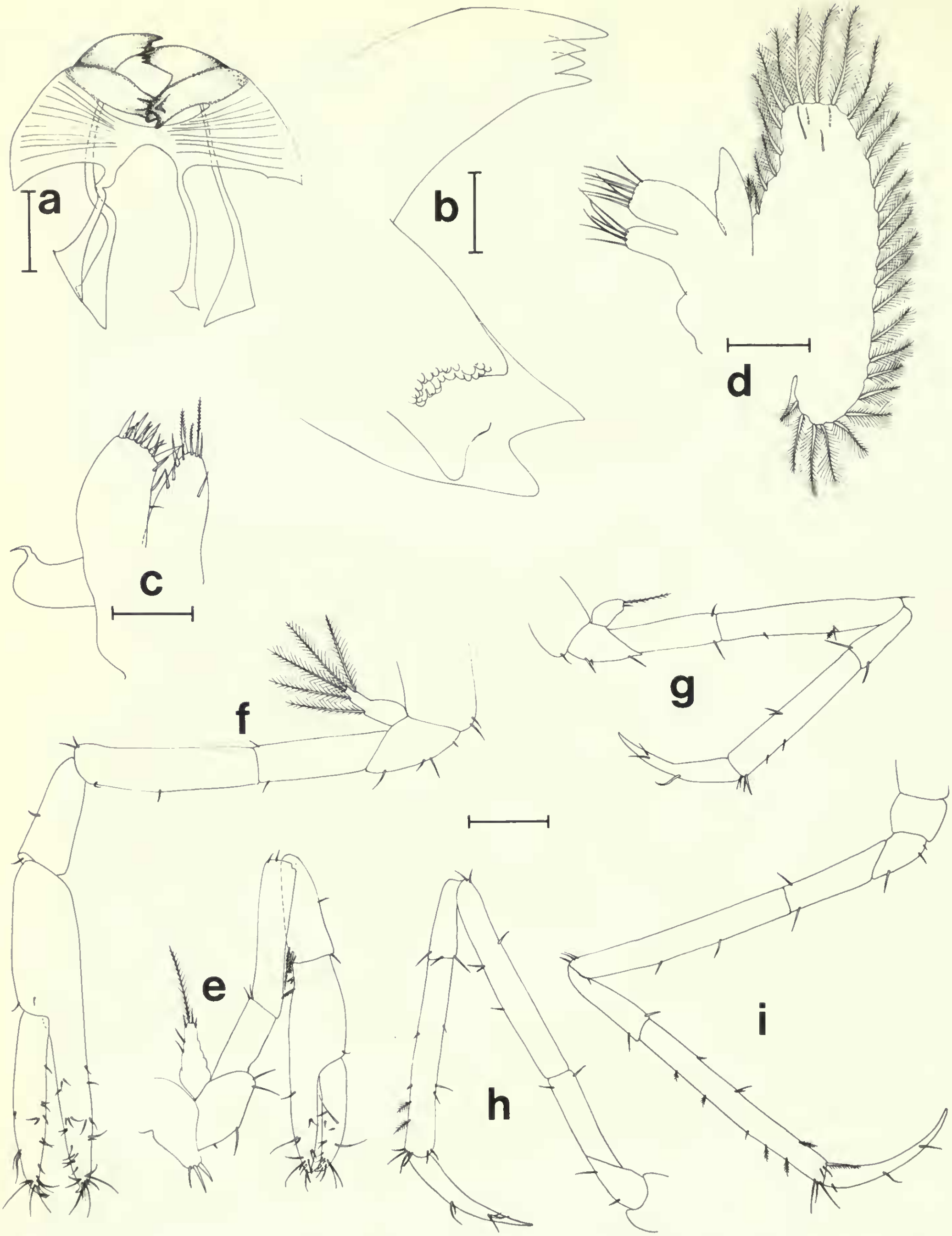

Fig. 16 Post larva 1: (a) mandibles and musculature; (b) mandible with *pars incisiva* (above) and *pars molaris* (below); (c) maxilla 1; (d) maxilla 2; (e) pereiopod 1: (f) pereiopod 2; (g) pereiopod 3; (h) pereiopod 4; (i) pereiopod 5. a, e–i = 0·2 mm; c, d = 0·1 mm; b = 0·05 mm.

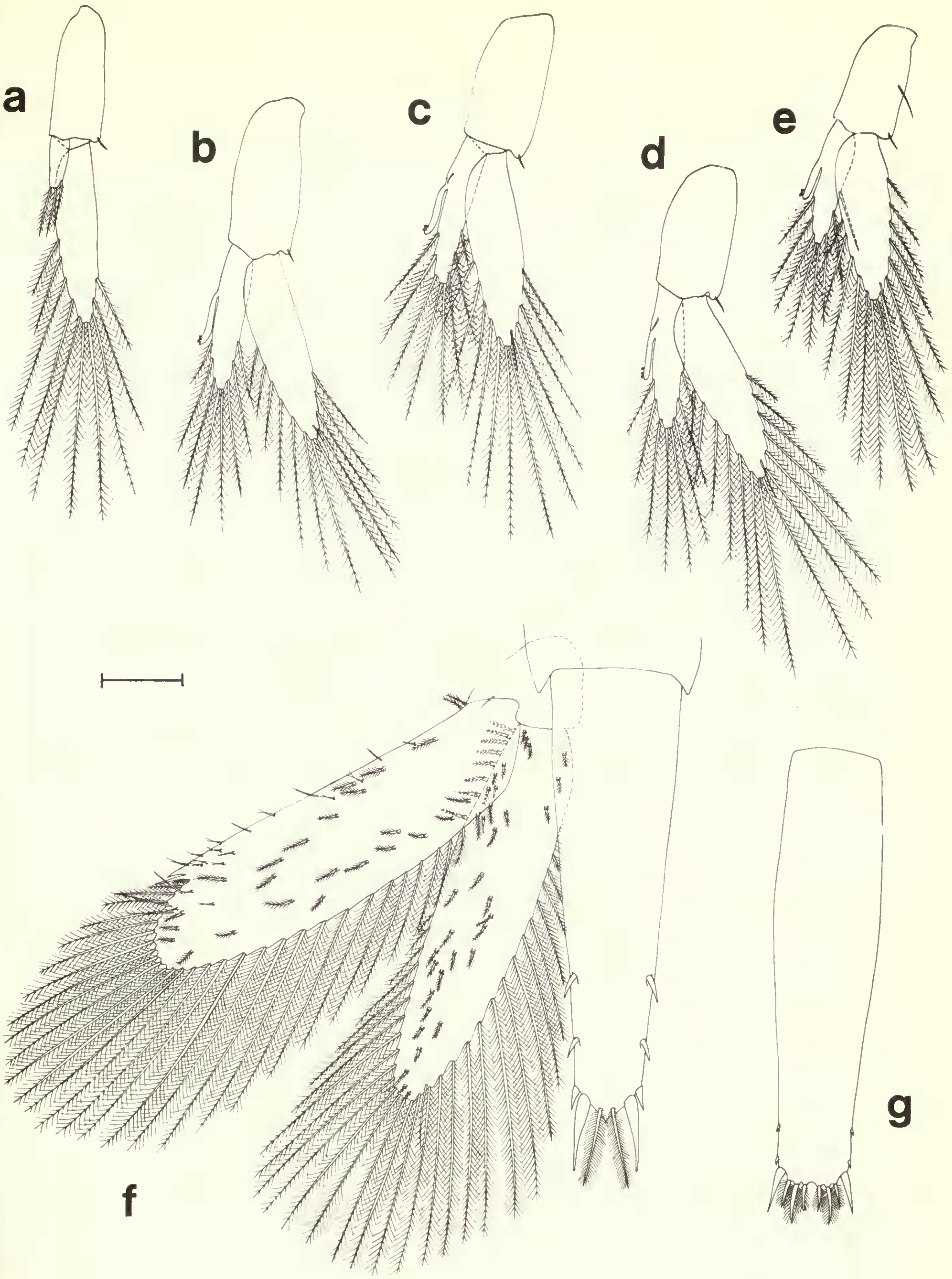

Fig. 17. Post larva 1: (a) pleopod 1; (b) pleopod 2; (c) pleopod 3; (d) pleopod 4; (e) pleopod 5; (f) telson. Intermediate stage: (g) telson. Bar scale = 0·2 mm.

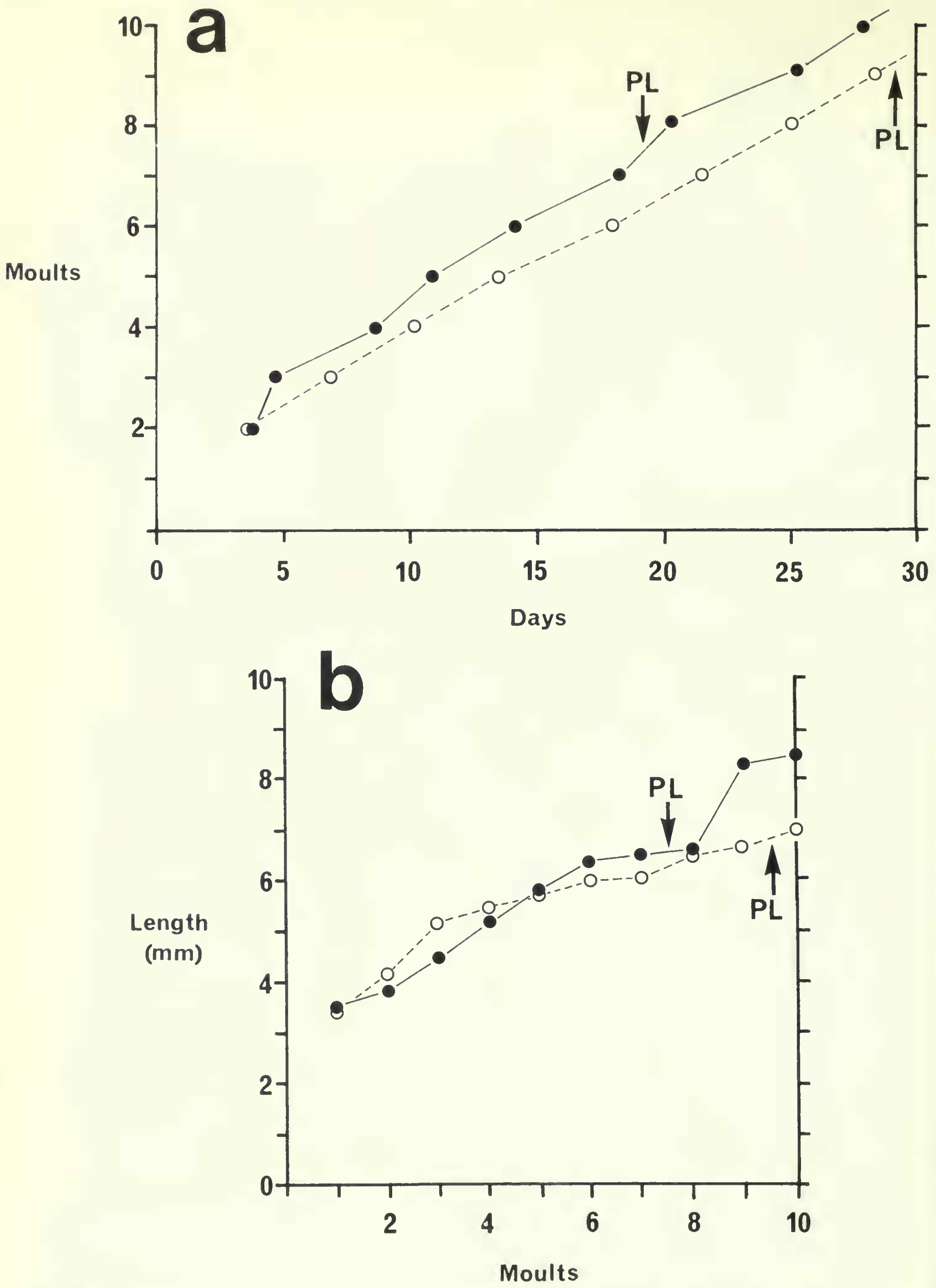

Fig. 18 Effect on (a) intermoult period, (b) growth rate of larvae reared with (○ - - - - - ○) and without (●——●) antibiotic. Figures averaged from 10 individuals at each stage.

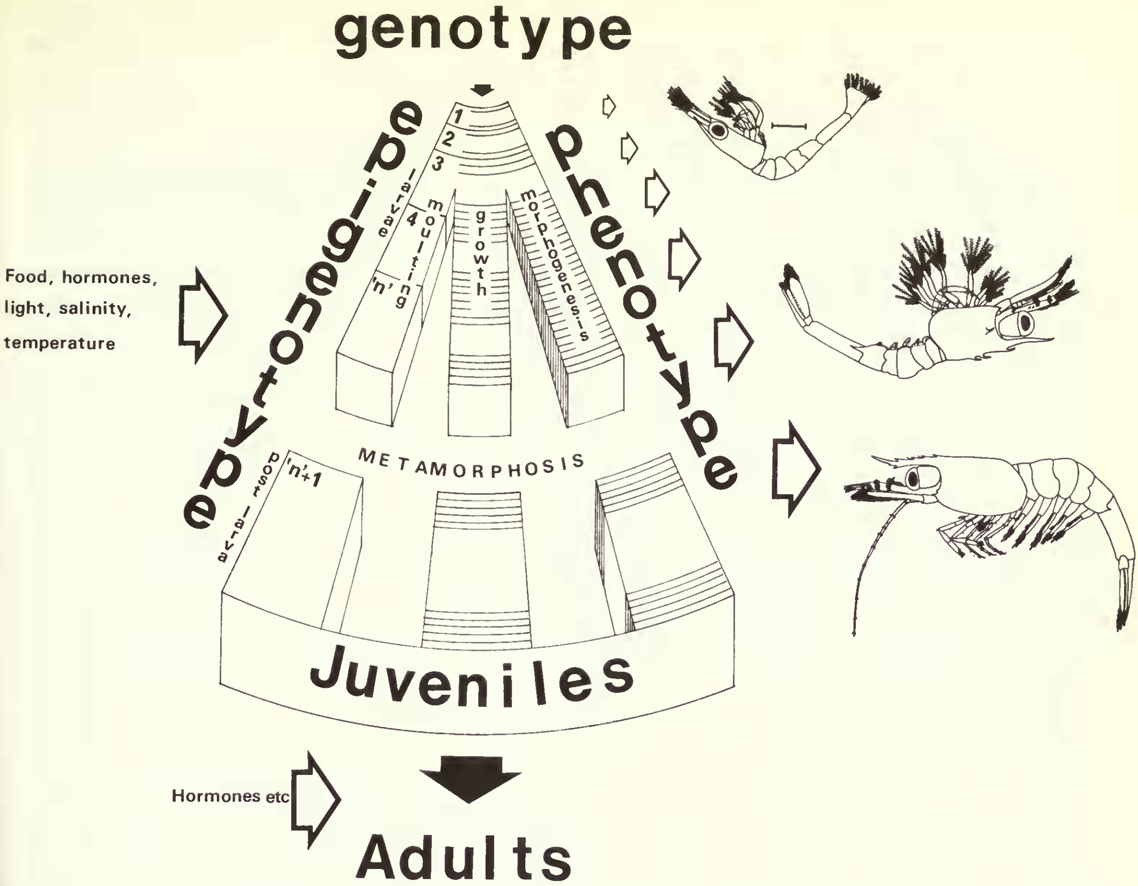

Fig. 19 Larval development of decapod Natantia showing the relationship between genetic input, epigenesis and the internal and external environmental factors which affect the semi-independent developmental processes of moulting, growth and morphogenesis. This results in larval phenotpyic variation in morphometric and meristic characters and in the number of stages. The system stabilizes in the post larva after metamorphosis. Bar scale = 0·5 mm.

Discussion

Effect of antibiotic on morphogenesis

The results of detailed comparisons of moults and larvae at each stage from specimens reared with (+AB) and without (−AB) antibiotic are shown in Table 1. There was no appreciable effect on normal phenotypic variation. However, there was a noticeable effect on the average intermoult period, which in −AB larvae was 2·9 days while in +AB larvae it was 3·5 days (Fig. 18a). This is the reverse of the situation in the brachyuran *Hyas araneus* (Linnaeus) in which the intermoult period was shortened at both 10 and 15 °C at the same concentration of antibiotics used in the present work (Christiansen, 1971). Christiansen also found that mortality of laboratory reared larvae was lower when antibiotics were used. This effect was not found in *Palaemon* (*Palaemon*) *longirostris;* 92% survival was recorded in −AB larvae but only 71% in +AB larvae. In two experiments made with two replicate populations of 100 and 25 larvae of *Palaemon serratus*, Wickins (1972) found that stocking densities did affect total percentage survival but that the addition of antibiotics had little effect on survival (100 larvae/litre: −AB 59% survival, +AB 58%; 25 larvae/litre: −AB 88%, +AB 86% from Wickins, 1972). The moult to post larvae in *P.* (*P.*) *longirostris* in the present work was delayed by about 10 days after two further moults had occurred in +AB larvae. Wickins also found that during the first 5–7 days of metamorphosis in each trial, more (average 28%) larvae had metamorphosed at any given time in the cultures without antibiotics. It was considered that either the presence of antibiotics or their bactericidal action was responsible for retarding the development of the larvae.

In the present work it was found that the effect of antibiotics on growth changed during the course of larval development (Fig. 18b). The initial increase in size by +AB larvae over −AB larvae may be a direct result of bacterial infection in the cultures. In the open sea the numbers of bacteria are low and it seems likely that this is correlated with a lack of solid surfaces on which to settle (Walne, 1958). In the compartmented rearing trays used in this study there is a high surface to volume ratio and bacteria are introduced into the trays both on the larvae themselves and on the *Artemia* nauplii used as food. It seems likely, therefore, that the unnatural stress introduced by the build-up of bacteria is successfully counteracted initially by the use of antibiotics and actually enhances growth compared with the −AB larvae. That this increased growth is not maintained may be due to a number of factors but one which might repay further investigation would be an assessment of the effect on the populations of gut flora. This would adversely affect food absorption and consequently growth. At the eighth moult both the +AB and −AB larvae are similar in size. This apparent slowing of growth in −AB larvae occurs after the majority of specimens have moulted to post larvae. Much internal reorganization takes place in connection with the change in the swimming mode. The upside down, tail first, thoracic exopodite swimming and planktonic mode of life is replaced by a basically benthic mode, and when swimming occurs the post larva is the right way up, head first and uses abdominal pleopods. The internal changes have been monitored by Campillo *et al.* (1975) who found that during larval development the growth process in *Palaemon serratus* (Pennant) alternates between periods of hyperplasy (stages 1–4, 5–7) and hypertrophy (stages 4–5, 7 to post larva). Prior to the post larval moult any growth is by an increase in cell size rather than from an increase in cell number. Regnault (1971) found that free amino acids had two peaks during the larval development of *Crangon septemspinosa* Say at stage 3 and last larval stage. These biochemical and cellular changes tie in with two major periods of morphogenesis, i.e. the development of uropods and the loss of the thoracic swimming exopods and their replacement with abdominal swimming pleopods. Morphogenesis of the mouthparts (compare Figs 12c, d, e and 16a, b, c, d), necessitated by the change in diet, accompany these other changes in the mode of propulsion at the post larval moult. Hence at this moult there is unlikely to be much spare energy for growth. Once this first post larval moult is passed, growth rate increases and is faster in these −AB individuals than at any time during the development of either +AB or −AB larvae.

The process of development

Moulting, growth and morphogenesis in the early stages of natant development are synchronous. For the first few moults phenotypic variation is small or even absent, for example the number of plumose setae on the exopodite of antenna 2 in zoea 1 is 9, while in maxilla 2 the figures are 5 and 7 for zoeae 1 and 2 respectively (Table 1). Both size and morphology of these early stages are largely predictable. However, in later larval development there is some independence of the three development processes (Fig. 19). This results in variable numbers of stages and larvae of intermediate stage morphology in both plankton and laboratory reared material. This variability has been recorded in the Palaemonidae by Faxon (1879), Gurney (1924*a*), Gurney & Lebour (1941), Broad (1957*a*), Tsurnamal (1963), Little (1969) and Fincham (1977, 1979).

Knowlton (1974) in his hierarchical representation of energy flow in caridean larval development gives high priority to general maintenance and survival, moulting is placed next followed by the synthetic processes of growth, morphogenesis and regeneration which are given equal weight. The genetic content of the fertilized egg is fixed and the embryos and larvae develop through a series of 'causal relations' (Waddington, 1953). This epigenesis may be influenced by a number of factors including food (Broad, 1957*b*; Reeve, 1969; Knowlton, 1974), hormones (Hubschman, 1963; Costlow, 1968; Little, 1969), light (Knowlton, 1974), salinity and temperature (Sandifer, 1973; Knowlton, 1974). The virtual independence of the development processes is shown diagrammatically in Fig. 19. Larvae of similar moulting history may be quite different in size within certain limits (see size ranges in section on description of larval stages) and in general morphology. In contrast, the moult is a definitive event and this is represented on the left of the diagram by single lines at the time of each ecdysis. In the centre of the diagram growth is shown with a limited range of values at a given moult. The right of the diagram is evenly divided after stage 3 indicating the continuous process of morphogenesis, 'arrested' at intervals by the hard exoskeleton.

This model for prawn and shrimp development does not apply to all decapods. Knowlton (1974) states that 'Instances of variability are less frequently encountered in Macrura and Anomura, rarely in Brachyura'. The short larval phase of these groups produces a fixed number of moults which are usually morphologically distinct, comparable with the early stages in natant development. Knowlton further speculated that, in general, the degree of larval variation is an index of primitiveness. In the past the phylogeny of the Euphausiacea and Decapoda has been based largely on adult characters but in the light of more larval data it will be possible to re-examine existing classifications and test Knowlton's hypothesis.

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References

Broad, A. C. 1957*a*. Larval development of *Palaemonetes pugio* Holthuis. *Biol. Bull. mar. biol. Lab. Woods Hole* **112** (2) : 144–161.

—— 1957*b*. The relationship between diet and larval development of *Palaemonetes*. *Biol. Bull. mar. biol. Lab. Woods Hole* **112** (2) : 162–170.

Campillo, A., Regnault, M. & Luquet, P. 1975. Évolution de acides nucléiques au cours du développement larvaire de la crevette rose *Palaemon serratus* (Pennant). *Rev. Trav. Inst. Pêch. marit.* **39** (3) : 333–342.

Christiansen, M. E. 1971. Larval development of *Hyas araneus* (Linnaeus) with and without antibiotics (Decapoda, Brachyura, Majidae). *Crustaceana* **21** (3) : 307–315.

Costlow, J. D. 1968. Metamorphosis in crustaceans: 3–41. In: **Etkin, W. & Gilbert, L. I.** (eds), *Metamorphosis: a problem in developmental biology*. North Holland Publishing Co. Amsterdam.

Cviic, V. The bacterial and bacteriostatical action of antibiotics on marine bacteria. 1. Penicillin and streptomycin. *Acta adriat.* **5** (7) : 135–166.

Czerniavsky, W. 1884. Crustacea Decapoda Pontica littoralia. Materialia ad Zoographiam Ponticam comparatam. II. *Trans. Soc. Univ. Kharkow* **13** (suppl.) : 1–268.

Edwards, H. Milne 1837. Histoire naturelle des Crustaces. II. Paris 531 pp.

Faxon, W. A. 1879. On the development of *Palaemonetes vulgaris*. *Bull. Mus. comp. Zool. Harv.* **5** : 303–330.

Fincham, A. A. 1977. Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia). 1. Laboratory methods and a review of *Palaemon* (*Palaeander*) *elegans* Rathke, 1837. *Bull. Br. Mus. nat. Hist.* (Zool.) **31** (1) : 1–28.

—— 1979. Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia). 2. *Palaemonetes* (*Palaemonetes*) *varians* (Leach, 1814) and morphological variation. *Bull. Br. Mus. nat. Hist.* (Zool.) **35** (2) : 163–182.

—— **& Williamson, D. I.** 1978. Crustacea, Decapoda: Larvae. VI Caridea, Families Palaemonidae and Processidae. *Fich. Ident. Zooplancton*, 159/160 : 8 pp.

Gurney, R. 1923. Some notes on *Leander longirostris* M. Edwards, and other British prawns. *Proc. zool. Soc. Lond.* 97–123.

—— 1924*a*. The larval development of some British prawns (Palaemonidae) – I. *Palaemonetes varians*. *Proc. zool. Soc. Lond.* 297–328.

—— 1924*b*. The larval development of some British prawns (Palaemonidae). II. *Leander longirostris* and *Leander squilla*. *Proc. zool. Soc. Lond.* 961–982.

— & **Lebour, M. V.** 1941. On the larvae of certain Crustacea Macrura, mainly from Bermuda. *J. Linn. Soc. Lond., Zool.* **41** : 89–181.

Heller, C. 1863. Die Crustaceen des südlichen Europa. Crustacea Podophthalmia. Wilhelm Braumüller, Wien. x, 336 pp.

Holthuis, L. B. 1950. The Palaemonidae collected by the Siboga and Snellius expeditions with remarks on other species. 1. Subfamily Palaemoninae. *Siboga Exped.* **39a** : 1–268.

Hubschman, J. H. 1963. Development and function of neurosecretory sites in the eyestalks of larval *Palaemonetes* (Decapoda : Natantia). *Biol. Bull. mar. biol. Lab. Woods Hole* **125** : 96–113.

Knowlton, R. E. 1974. Larval developmental processes and controlling factors in decapod Crustacea, with emphasis on Caridea. *Thalassia jugosl.* **10** (1/2) : 138–158.

Korschelt, E. 1944. Ontogenie der Decapoden. *Bronns Kl. Ordn. Tierreichs* **5** (1) Bk **7**, Decapoda No. 6 : 671–861.

Little, G. 1969. The larval development of the shrimp, *Palaemon macrodactylus* Rathbun, reared in the laboratory, and the effect of eyestalk extirpation on development. *Crustaceana* **17** : 69–87.

Man, J. G. De 1915. On some European species of the genus *Leander* Desm., also a contribution to the fauna of Dutch waters. *Tijdschr. ned. dierk. Vereen.* Ser. 2, **XIV** : 115–179.

—— 1923. *Leander longirostris* (H. M.-Edw.) var. *robusta* nov. var., the common prawn of the estuary of the Meuse and of the Hollandsch Diep. *Tijdschr. ned. dierk. Vereen.* Ser. 2, **XIX** (1) : 1–9.

Reeve, M. R. 1969. Growth, metamorphosis and energy conversion in the larvae of the prawn, *Palaemon serratus*. *J. mar. biol. Ass. U.K.* **49** : 77–96.

Regnault, M. 1971. Acides aminés libres chez les larves de *Crangon septemspinosa* (Caridea). Variation de leur taux de l'éclosion à la métamorphose. Leur rôle au cours du développement et leur importance dans la nutrition. *Mar. Biol. Berlin* **11** (1) : 35–44.

Sandifer, P. A. 1973. Effects of temperature and salinity on larval development of grass shrimp, *Palaemonetes vulgaris* (Decapoda, Caridea). *Fishery Bull. natn. ocean. atmos. Adm.* **71** : 115–123.

Tsurnamal, M. 1963. Larval development of the prawn *Palaemon elegans* Rathke (Crustacea Decapoda) from the coast of Israel. *Israel J. Zool.* **12** (1–4) : 117–141.

Waddington, C. H. 1953. Epigenetics and evolution. *Symp. Soc. exp. Biol.* **7** : 186–199.

Walne, P. R. 1958. The importance of bacteria in laboratory experiments on rearing the larvae of *Ostrea edulis* (L.). *J. mar. biol. Ass. U.K.* **37** : 415–425.

Wickins, J. F. 1972. Developments in the laboratory culture of the common prawn *Palaemon serratus* (Pennant). *Fishery Invest., Lond.*, Ser. 2, **27** (4) : 23 pp.

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